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PROLIFIC DEVELOPMENT OF PACHYTHECALIINES IN LATE BARREMIAN, BULGARIA: CORAL TAXONOMY AND SEDIMENTARY ENVIRONMENT

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Abstract: Diversified and abundant corals of the suborder Pachythecaliina (order Hexanthiniaria) are described from Upper Barremian, biostromal reefs of the Emen Formation, Lovech Urgonian Group, north central Bulgaria. The corals are mostly of the phaceloid growth form and represent 14 species (six new), 12 genera (three new), belonging to five families. Pachythecaliines occur with the small, monopleurid cylindrical rudist *Mathesia darderi*. The rudists frequently are densely clustered, occur between coral branches or are in contact with them. Other corals, with the exception of the phaceloid *Calamophylliopsis*, and other rudists, are rare. Non-laminated microbialite crusts provided additional, structural support for bioconstruction development. Microbialites (automicrites) can be interpreted as a product of microbial activity, or alternatively, as a result of carbonate precipitation, brought about by non-living organic substrates (organomineralization *s.s.*). In addition to microbialites, metazoans are encrusted by heterotrophic skeletal microorganisms, while photophilic and oligotrophic microencrusters, usually common in other coral-bearing limestones of the Emen Formation, are very rare. The section at the Rusalya Quarry (NW of Veliko Tarnovo), about 42 m thick, provides the sedimentary and environmental context for the reefal biostromes. The vertical biotic and sedimentary succession displays a general shallowing trend: from the outer carbonate platform with bioclastic limestones containing small boundstone patches (corals, but not pachythecaliines, *Lithocodium aggregatum*), to the inner platform with rudist biostromes. The pachythecaliine-rich biostromes, 2.5 m thick, were developed in a low-energy environment, referred to the distal part of the rudist-dominated area of the platform. The development of microbialites was facilitated by a low sedimentation rate, and possibly by increased nutrient level. Only poorly diversified and non-phaceloid pachythecaliines occur in other coral-rich limestones and marls of the Urgonian complex in Bulgaria. The assemblage described is the most remarkable, Early Cretaceous coral community worldwide, with regard to pachythecaliines. Phaceloid pachythecaliines are only more common in the Upper Jurassic rocks, being particularly diversified in the Tithonian–Lower Berriasian Štramberk Limestone (Czech Republic) and its equivalent in the Polish Outer Carpathians. However, their sedimentary context differs from that described for the corals of the Emen Formation.

Key words: corals, taxonomy, carbonate platform, palaeoecology, Cretaceous, Fore-Balkan, Bulgaria.

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INTRODUCTION

Pachythecaliina Eliášová, 1976 (= Amphiastraeina Alloiteau, 1952) is an extinct suborder (Late Triassic–Late Cretaceous) that has focussed the attention of coral researchers in the context of the origin of corals from the order Scleractinia Bourne, 1900 in the Middle Triassic, and their possible relationship to the order Rugosa Milne-Edwards et Haime, 1851. Many pachythecaliines display "archaic", skeletal features, which are unique among post-Palaeozoic corals. These corals usually were or still are classified in the Scleractinia. However, because of their skeletal architecture, especially in the Late Triassic Zardinophyllidae Montanaro Gallitelli, 1975 and the Jurassic–Cretaceous Amphiastraeidae Ogilvie, 1897 – similar to the late Palaeozoic plerophyllines – some authors classified them directly into the Rugosa (Koby, 1888; Ogilvie, 1897) or assumed their rugosan ancestry (Cuif, 1975, 1977, 1981, 2010; Melnikova and Roniewicz, 1976; Stolarski, 1996). Alternatively, pachythecaliines (in a narrow or broad meaning) were

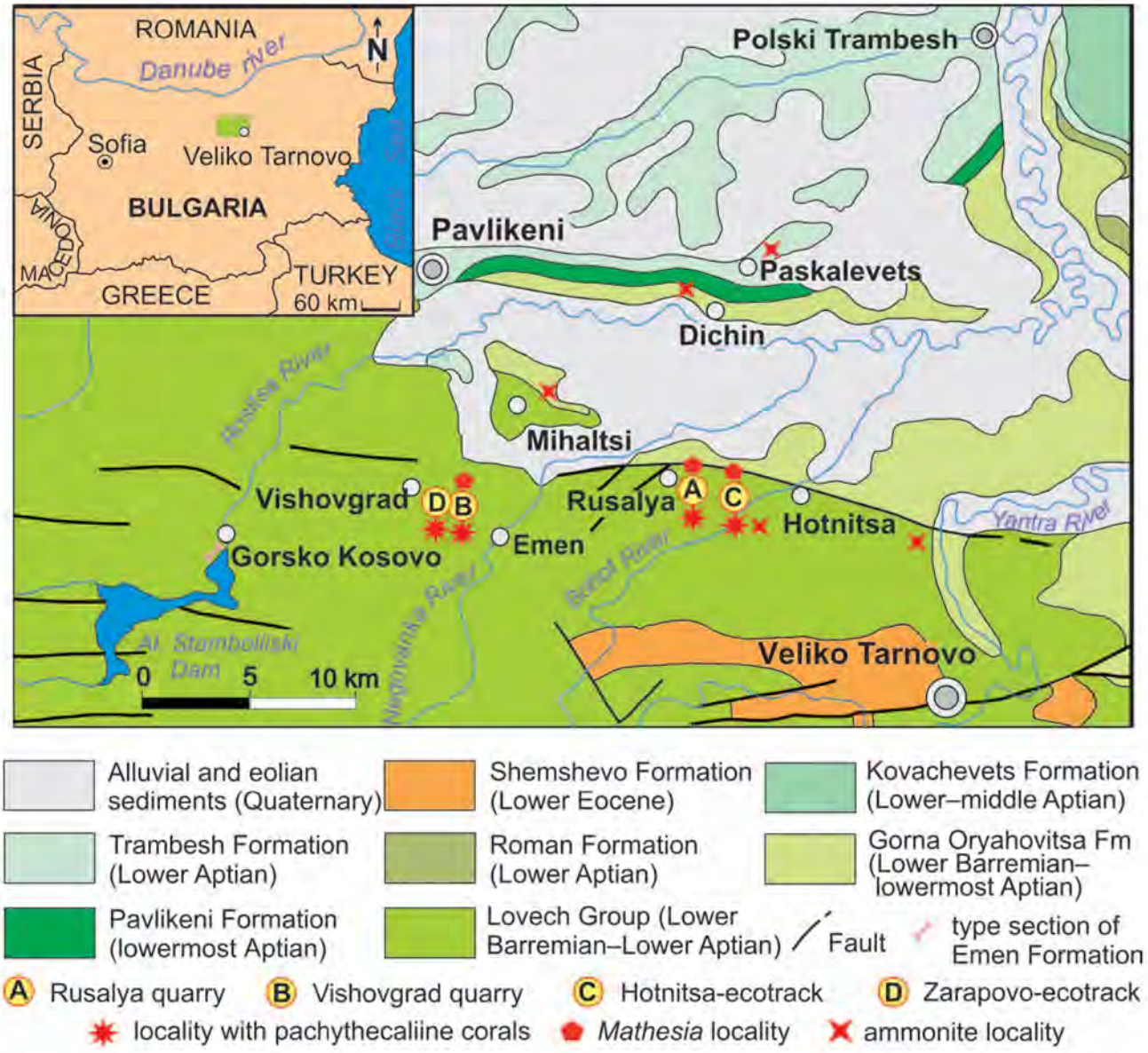


Fig. 1. General location of study area on geological map (1: 500 000) (after Cheshitev *et al.*, 1989; modified and corrected) with location of sampling sites for corals, rudists *Mathesia darderi*, as well as ammonites, used for local biostratigraphy

classified as the separate order Hexanthiniaria Montanaro Gallitelli, 1975 (Montanaro Gallitelli, 1975; Eliášová, 1976b, 1978; Roniewicz, 2008; Melnikova and Roniewicz, 2012; Morycowa, 2012).

Phaceloid (branched, built of parallel corallites, pseudocolonial) pachythecaliine corals were moderately common in the Late Jurassic and locally diversified taxonomically (Tithonian–Lower Berriasian Štramberk Limestone), but were rare during the Cretaceous. The coral communities, dominated by diversified, phaceloid pachythecaliines, recently discovered in the Upper Barremian limestones of the Emen Formation in north central Bulgaria (Kołodziej *et al.*, 2009, 2011b), are unique among post-Jurassic coral communities. The aims of this paper are the taxonomic and palaeoecological analysis of these corals, as well as the interpretation of the sedimentary environment of pachythecaliine-rich bioconstructions in the Emen Formation.

GEOLOGICAL SETTING AND MATERIAL

During the Barremian–Early Aptian several carbonate platforms existed on the northern, Tethyan margin, located in the present territory of Bulgaria (Lovech Urgonian Group, Vratsa Urgonian Group, Russe Formation). In particular, the Lovech Urgonian Group in the central Fore-Balkan (north central Bulgaria) contains diverse coral and rudist assemblages. This Urgonian complex consists of four terrigeneous and four carbonate formations (Figs 1, 2; Khrischev, 1966; Nikolov, 1969; Peybernès *et al.*, 1998; review in Minkovska *et al.*, 2002; Nikolov *et al.*, 2007). Coral communities – from level-bottom assemblages to coral-microbialite reefs – represent both clear- and turbid-water environments. Up to now, more than 100 coral species were described, mainly from soft marls, but were analysed more rarely with respect to their palaeoecology (e.g., Toula, 1889;

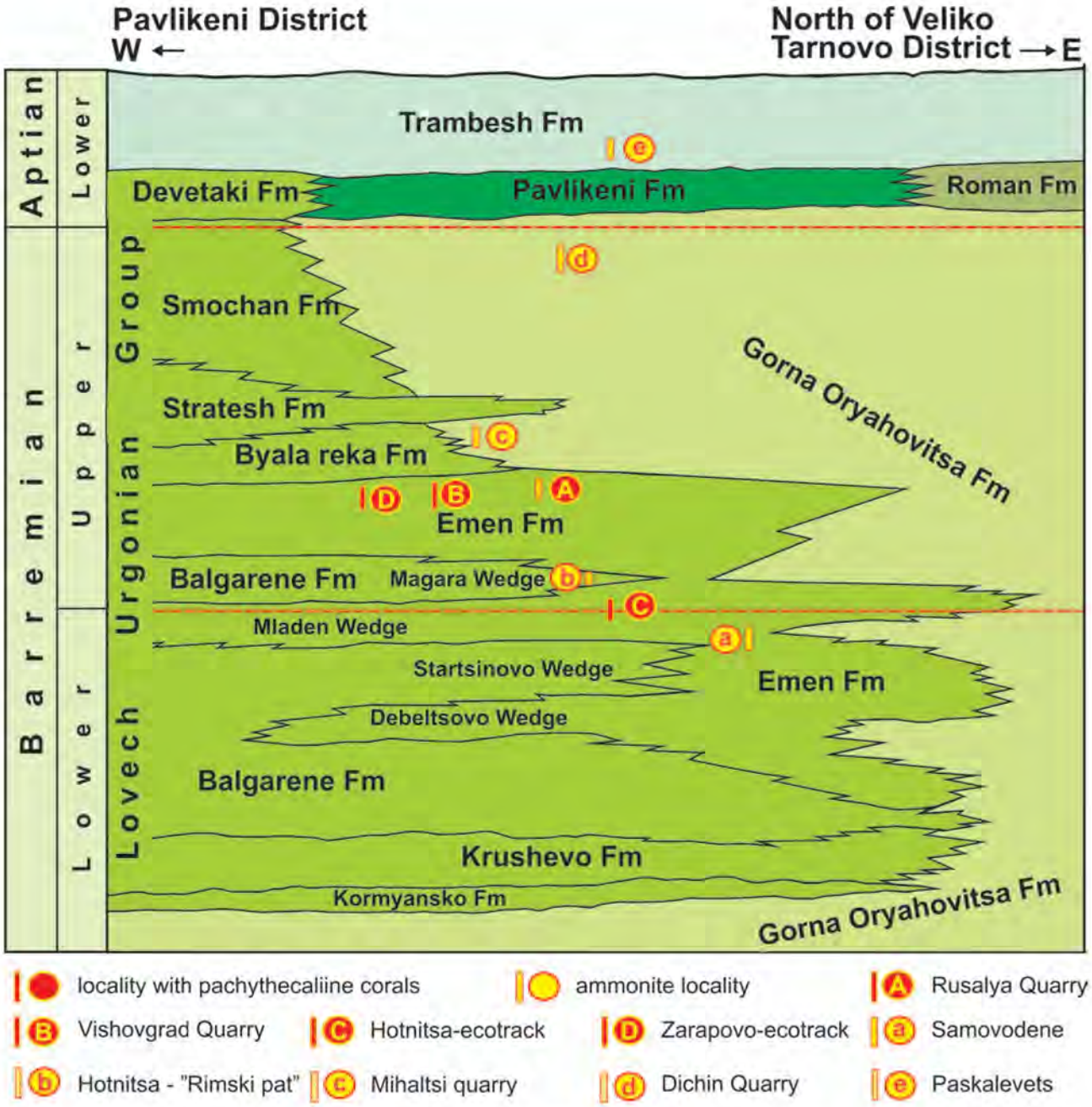


Fig. 2. Lithostratigraphic scheme of study area and stratigraphic position of sampling sites

Zlatarski, 1967, 1968a, b, c; Tchechmedjieva, 2001; Idakieva, 2002, 2003, 2007, 2008; Idakieva and Ivanov, 2002; Kołodziej *et al.*, 2007; see also Ilcheva and Motchurova-Dekova, 2011). Diversified coral assemblages occur also in pure or marly limestones (Kołodziej *et al.*, 2011c). However, apart from the present paper, they have not yet been the subject of detailed, taxonomic publications.

The pachythecaliine corals studied occur in limestones of the Emen Formation in the Veliko Tarnovo (also translitterated as Veliko Turnovo, Veliko Trnovo, Veliko Tyrnovo) area. They were collected mainly in quarries at Rusalya and Vishovgrad. Sampling was supplemented in the Zarapovo-ecotrack and Hotnitsa-ecotrack, referred to below as Zarapovo and Hotnitsa, respectively (Fig. 1). This study also includes samples from Veliko Tarnovo, or its immediate vicinity, referred to below as Veliko Tarnovo, collected by the late Prof. Ryszard Marcinowski (Warsaw University), but the exact collecting location is unknown.

The Emen Formation, situated in the middle part of the Lovech Urgonian Group, was established by Khrischev (1966) in the region of Emen village, about 20 km NW of Veliko Tarnovo (Fig. 1). The best outcrops of this formation occur between the Osum and Jantra Rivers, and the type section is located at the Alexander Stambolijski Dam near to Gorsko Kosovo village, 40 km west of Veliko Tarnovo. Previous studies showed that the limestones of the Emen Formation were deposited on a shallow-water, carbonate platform, largely in an open lagoon. Intercalations of siliciclastic sediments are relatively rare (Khrischev, 1966; Khrischev and Bakalova, 1974). Microfacies analyses, performed by Min-

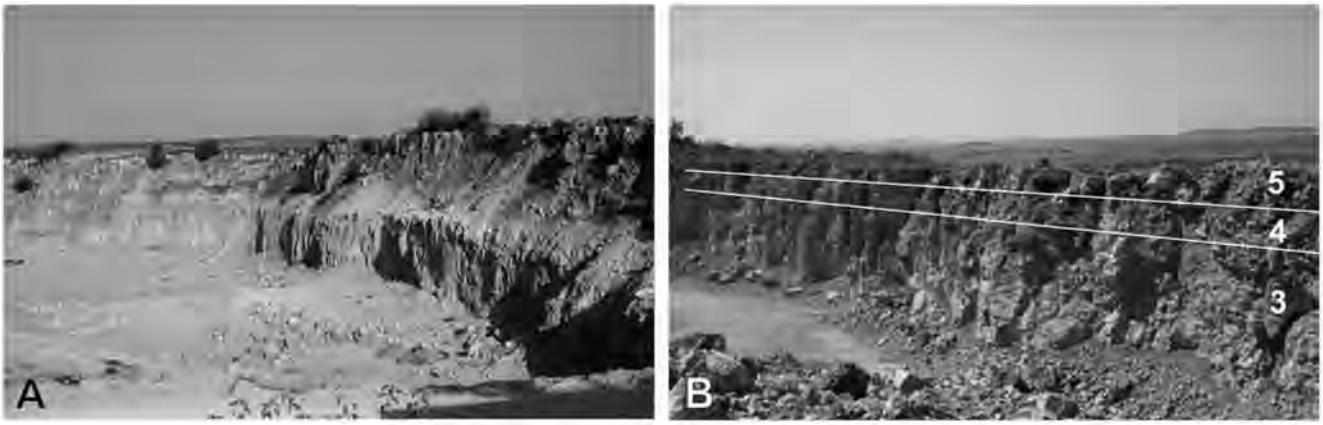


Fig. 3. General view of Rusalya Quarry. **A** – view of south wall, showing lowermost part of section with units 1, 2 and part of unit 3. Maximum height of wall is about 30 meters. **B** – view of WNW wall with approximate boundaries between units 3, 4 and 5. Straight line does not reflect exact relief of pachythecaliine-*Mathesa* biostrome. Depression behind quarry is built of siliciclastics of Gorna Oryahovitsa Formation

kovska (1996) in three sections revealed sediments of (1) the inner platform (the Preobrazhenski Monastir section – close to Veliko Tarnovo; cored wells), (2) external parts of the inner platform (the area around Emen village), and (3) various facies, representing the distal to the inner part of the carbonate platform (Alexander Stambolijski Dam section). In the Emen Formation bioclastic and coral-bearing limestones dominate, while rudist occurren- ces are uncommon (Minkovska, 1996). The section in Rusalya was studied for the first time by the present authors (see Fenerci-Masse *et al.*, 2011).

In the study area, the Emen Formation grades laterally into the siliciclastic Gorna Oryahovitsa Formation (Figs 2, 3B). The Emen Formation consists here of two tongues bracketed by marly units with ammonites appearing to correspond to the upper part of the Lower Barremian (probably Kotetishvilia compressissima Zone) and the middle part of the Upper Barremian (Gerhardtia sartousiana Zone) (Khrischev, 1992; Ivanov, 1995; Ivanov and Nikolov, 1995; Stoykova and Ivanov, 2000; Ivanov and Idakieva, 2009; see also Fenerci-Masse *et al.*, 2011).

The stratigraphy of the sampling sites ranges from the early Late Barremian (Toxancyloceras vandenheckii Zone; site Hotnitsa) up to the early middle Late Barremian (Gerhardtia sartousiana Zone; sites: Rusalya and Vishovgrad Quarries, Zarapovo). The presence of the latest Early Barremian Moutoniceras moutonianum Zone in Hotnitsa cannot be ruled out.

More detailed studies of the sedimentary succession were performed in the Rusalya Quarry. The Vishovgrad Quarry was inaccessible for detailed studies. Microfacies studies were performed on thin sections from all sampling sites. The results, presented here, are based on the study of 136 thin sections; 94 thin sections are of standard size (4 × 2.7 mm) and 42 are large (6 × 5 mm). The specimens are deposited at the Institute of Geological Sciences, Jagiellonian University, Kraków (collection UJ 225 P). Twenty thin sections from three samples, collected by the late Prof. R. Marcinowski, are housed at the Institute of Palaeobiology, Polish Academy of Sciences, Warszawa (collection abbreviated as ZPAL Bułg).

SEDIMENTARY SUCCESSION AT RUSALYA QUARRY

As noted above, more detailed studies of the sedimentary succession bearing pachythecaliine-rich biostromes were performed only in the Rusalya Quarry. In the following chapter the results of field observations and microscopic analysis of the material from all sites are presented.

Sedimentological studies at Rusalya were carried out on a well-exposed section, about 42 m thick (Fig. 3). The section consists of five main, lithological units (Fig. 4):

(1) ~10 m. Bioclastic packstone, rarely wackestones and grainstones, containing small, decimetre-scale boundstone patches, with irregular rims, built of small corals and calcified sponges, encrusted by *Lithocodium aggregatum* and microbial structures with vesicular, 'bacinellid' fabric (Fig. 4A, B). Colonial corals and their fragments are small (usually no more than a few centimetres in size). Associated biota include calcified sponges (chaetetids, stromatoporoids) and rare rudists. Pachythecaliine corals (or other phaceloid corals), abundant in the coral-*Mathesia*-microbialite biostromes (unit 4), have not been recognized in unit 1.

(2) ~15 m. Bioclastic limestones interlayered with rudist (mostly monopleurids) limestones (Fig. 4C).

(3) ~8 m. Packstone-dominated, bioclastic limestones with chaetetids, stromatoporoids, subordinately with rudists and small, colonial corals, but without pachythecaliines (Fig. 4D).

(4) ~2.5 m. Coral-rudist-microbialite biostromes and possibly also low-relief bioherms. The dominant metazoan components are large, phaceloid corals: pachythecaliines (Fig. 4E, see also Figs 11–13, 17–19, 22–24) and *Calamophylliopsis* sp. and small monopleurid rudists *Mathesia darderi* (Astre, 1933), densely clustered locally (e.g., Fig. 4F; see also Figs 5C, 6A). Microbialites are common (e.g., Fig. 7B, C, E; see also Fig. 23B, C). Access to the upper part of the section was difficult, therefore establishing a more detailed pattern of the lateral distribution of corals and rudists, as well as the lateral extension and geometry of bioconstructions (biostromes, low-relief bioherms), requires supple-

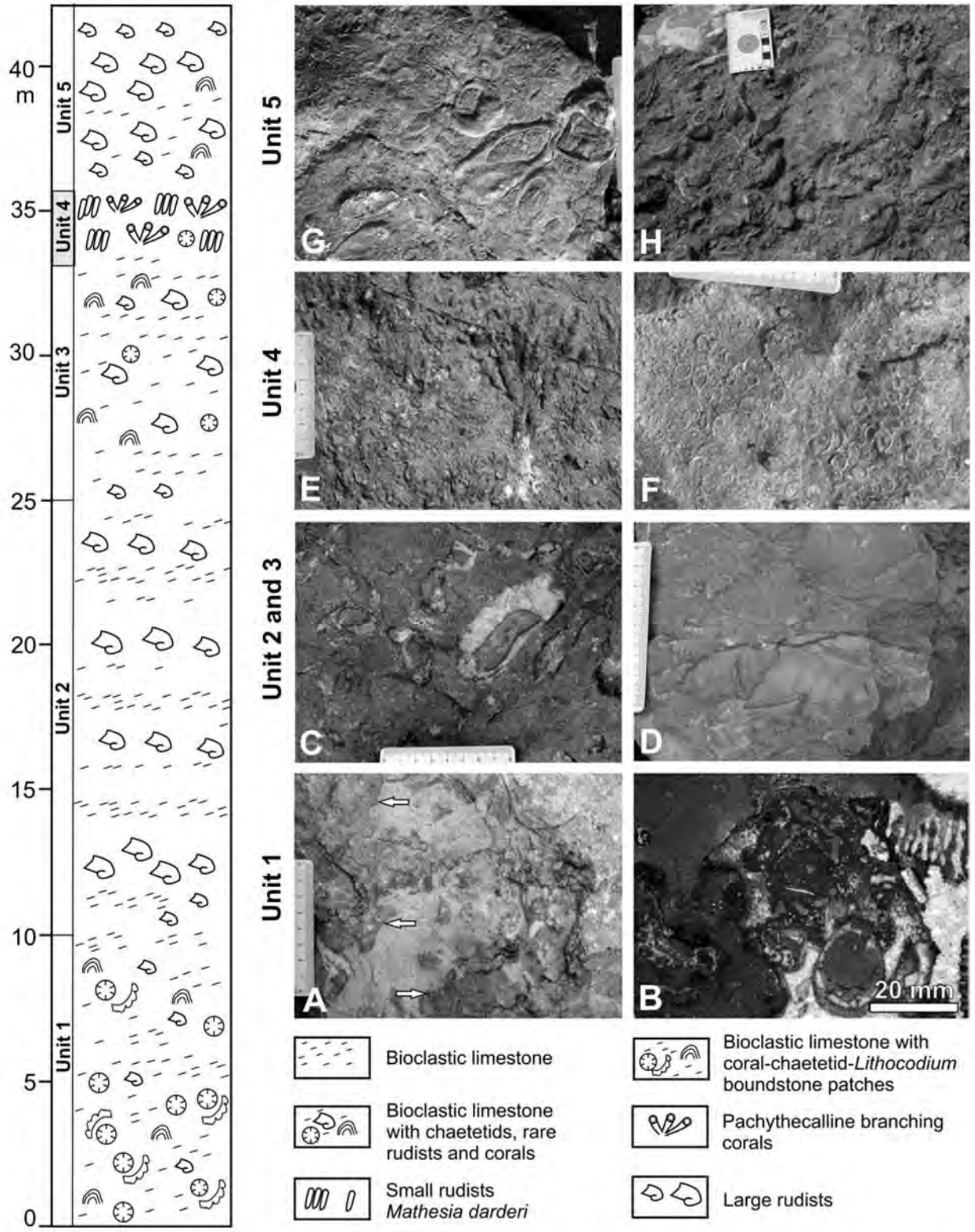


Fig. 4. Generalized lithostratigraphic section of Upper Barremian succession at Rusalya Quarry, showing main lithologic units, with examples of biofacies. **A, B** – unit 1: bioclastic limestone with small boundstone patches (arrows in A), built of small corals, calcified sponges, *Lithocodium aggregatum* (B) and 'bacinellid', microbial structures. **C** – unit 2: bioclastic limestone with monopleurid rudists. **D** – unit 3: bioclastic limestone with chaetetid sponges. **E, F** – unit 4: coral-rudist-microbialite biostrome with phaceloid pachythecaliine coral *Pleurophyllia* sp. (E) and monospecific, rudist cluster of *Mathesia darderi* (F). **G, H** – unit 5: rudist biostromes, built of dense aggregates of elongated, monopleurid rudists

mentary studies. Their detailed description, including microfacies analysis, is given in the next section.

(5) ~6 m. Rudist biostromes, built by dense aggregates of rudists, more diversified and larger in size than those in unit 4: large and small requieniids, elongated, monopleurids and possibly *Agriopleura* sp. (Fig. 4G, H; J.-P. Masse, pers. comm., 2012). Chaetetids occur subordinately.

PACHYTHECALIINE-RUDIST-MICROBIALITE BIOCONSTRUCTIONS

The simple term *biostrome* or *autobiostrome* (*sensu* Kershaw, 1994) can be used for the boundstones, analysed at Rusalya, because field observations indicate the bedded nature, although owning to difficult access to the upper part of the section at Rusalya, the occurrence of low-relief bioherms can not be excluded. The term *biostromal reef* is applied here, in accordance with the recent, broad approach to reef definition (Leinfelder *et al.*, 1994; Insalaco *et al.*, 1997; Wood, 1999; Stanley, 2001; Riding, 2002; Kiessling *et al.*, 2002; Kiessling, 2009; Flügel, 2010). The broad term *bioconstruction* represents a more inclusive term for more-or-less clearly recognizable structures (Höfling, 1997; Riding, 2002). This term is also used here, because determination of the exact morphology of reefal lithosomes (biostromes *versus* bioherms) was difficult, owing to the state of the outcrops at Zarapovo and Hotnitsa, and limited access for study in the Vishovgrad Quarry.

The descriptions of pachythecaliine-rudists- microbialite bioconstructions are based on field observations and microscopic studies (including the taxonomy of corals and some other fossils) mainly of samples from Rusalya and Vishovgrad. Pachythecaliines are clearly the most common and diversified corals in the bioconstructions studied (see Systematic Palaeontology, Figs 10–24): 14 species (six new, eight in open nomenclature), 12 genera (four new, three of them are distinguished formally). Large, phaceloid forms are often in growth position (Figs 4F, 5A, B). The most common (17 fragments of large coralla; 15 of them collected in Rusalya) is *Pleurophyllia bulgarica* sp. nov. reaching about 70 cm in height. In contrast to Rusalya, sampling at other sites was not extensive, which also reflected in the taxonomic diversity, namely at Rusalya: eight genera, nine species; at Vishovgrad: four genera, five species; at Hotnitsa: two genera, two species; at Zarapovo: one genus, one species. Analysis of 20 thin sections from three samples collected by the late Prof. R. Marcinowski at the unknown site at Veliko Tarnovo revealed three species of pachythecaliines, *Calamophyliopsis* sp. and one undetermined coral, thus showing a general, "taxonomic pattern" as the rich coral assemblages from Rusalya. Associated corals, except for *Calamophylliopsis* sp. are rare. These corals are small, and only the phaceloid *Calamophylliopsis* sp. attains a larger size of up to 40 cm (Fig. 8).

Apart from corals, the monopleurid rudist *Mathesia darderi* and microbialite crusts provided additional, structural support for reef development. Rudist assemblage is nearly monospecific, dominated by *M. darderi*, with small, cylindrical shells (50% of the average diameters ranging from 0.7 to 0.8 cm; Fenerci-Masse *et al.*, 2011) with the outer, calcitic shell layer and the inner one, aragonitic converted to neomorphic calcite (Fig. 6; Fenerci-Masse *et al.*, 2011, figs 5–7, 11; see also Masse and Fenerci-Masse, 2010). They frequently are clustered densely and occur between coral branches, or are attached directly to them (Figs 4F, 5C, 6, 12A, D, 14C, 16A; see also Fenerci-Masse *et al.*, 2011). Some small growth anomalies were observed in corals or rudists (Fig. 6C). Outside Rusalya, *M. darderi* is common at Vishovgrad and in samples from Hotnitsa (Fig. 5C). This species was also recognized in thin sections from samples, collected in Veliko Tarnovo by Prof. R. Marcinowski. They were not found at Zarapovo, but this may be due to sampling bias because, only limited sampling was performed at this site.

The corals and rudists are encrusted by microbialites, which occur also in semi-closed spaces (e.g., in interskeletal spaces between coral skeleton elements; Figs 7D, 23 A–B) and may partially (microbial "bridges", e.g., Figs 14C, D, 18F) or completely fill space between skeletons. Microbialites show dense, non-laminated micritic microfabric (Figs 7A–E, 8A, B), thus at the scale of microstructure can be categorized as pure leiolites. Poorly marked microlamination (Fig. 18A) and micropeloidal (mostly within microcavities; Fig. 9C, D) or clotted microfabrics was observed only locally. The crusts are termed here *microbialite*, but the more inclusive term *automicrite* can also be applied (see Microbialites in the chapter Palaeoenvironmental interpretation).

Microbialites are "pure", contain micrometre-scale "sparitic spots" of uncertain origin (small bioclasts?) or incorporate varying amounts of skeletal debris. In thin sections, microbialites are easy to distinguish from allomicrites by their dark colour (e.g., Figs 7A, D, 8A, B, 23B, C). Microbialites do not exhibit borings or encrusting microorganisms, either externally or internally, but fine burrowing traces are relatively common (Fig. 7B, C; compare with Fig. 9). Microbialite growth generated small cavities, locally with geopetal structures, filled with allochthonous micrite, calcite sparite cement, and rarely small grains (Figs 6A, 9). Bioclasts are rare in cavities, except for ostracods (Fig. 6E). Microbialite growth between skeletal elements (septa, wall, dissepiments) occurred only locally, "closed" interskeletal space, which prevented filling by sediment. Therefore, the space between skeletal elements is largely filled with calcite spar cement (e.g., Figs 5A, 10B, C, 12D, L, 13, 14C, 15D, 17A, 22B, C, H, 24B, C). Because septa are poorly preserved (usually only slightly micritized), observations of corallite morphology are difficult, particularly in vertical sections.

Small pyrite or orange-brown iron oxides (Fig. 7E), and locally also dolomite crystals are scattered within the microbialites, though very rarely within allomicrite in samples from Vishovgrad (Figs 8B, 15F). The surrounding sediment and biota appear unaffected by dolomitization, although in places the distinction between automicrite and allomicrite, if dolomitized, may be difficult. The presence of dolomite was supported by the standard staining of thin sections with Alizarin Red-S (see Adams *et al.*, 1984). In contrast to the calcite cement and allomicrite, dolomite remained unstained (Fig. 15F).

With regard to microfacies the pachythecaliine-bearing limestones from all of the sampling sites are similar. The associated sediment is calcimudstone, bioclastic wackestone and packstone. Quartz was observed only within the tests of some agglutinated foraminifera. Most metazoan bioclasts are fragments of small rudists (Figs 6A, 7A, 12B, 248A, B). Large metazoans, apart of corals and rudists, include sponges (calcified and non-rigid; Figs 8, 22A, E), and complete shells or fragments of small gastropods, recognizable mostly in thin sections (Figs 12A, 17A, C, D). Sponge spicules occur locally within the microbialites (Fig. 9A, B). Sponges, both non-rigid and calcified, show differential preservation even in spatially close parts of the same specimen (Fig. 9C, D, E). Well preserved skeletons may pass laterally to micropeloidal aggregates (Fig. 9C, D). Some structures may be relicts of sponge spicules (Fig. 9G, H). Other biota includes echinoderm plates, decapod crustacean appendages, similar to *Carpathocancer? plassenensis* (Schlagintweit et Gawlick, 2002) (Fig. 22G; cf. Schlagintweit *et al.*, 2007), small brachiopods, benthic foraminifera, including encrusting/cryptic forms (Figs 7F, H, 9F) and a few orbitolinids, ostracods (relatively common, particularly in microcavities, Fig. 7D, E), encrusting bryozoans, serpulids (Fig. 22A, F, G), *Girvanella*-like tubes and rare algae. This latter group includes dasycladacean green algae: *Zittelina hispanica* Masse, Arias et Vilas, 1993 (Fig. 18E), *Neomeris cretacea* Steinmann, 1899 (Fig. 18F), but mostly *Terquemella* sp., that is reproductive structures of undetermined large algae (I. I. Bucur, pers. comm., 2010). Crusts of coralline red algae were recognized only in two samples at Zarapovo. In contrast to the lower part of the section at Rusalya (Fig. 4B), thin crusts of *Lithocodium aggregatum* (*sensu* Schlagintweit *et al.*, 2010) and microbial structures with "bacinellid" fabric (*sensu* Maurin *et al.*, 1985; Schlagintweit and Bover-Arnal, 2013) with poorly developed vesicular meshwork, are rare (except in samples from Zarapovo) in most samples with pachythecaliines studied (Fig. 7F, G). Structures similar to and confused with *L. aggregatum*, recently reinterpreted as entobian borings (see section *Lithocodium/Bacinella* in the next chapter), associated with boring foraminfer *Troglotella incrustans* Wernli et Fookes, 1992 (Schmid and Leinfelder, 1996; Schlagintweit, 2012), were not recognized in the limestones studied. Large borings in metazoans, mostly *Entobia* sp., are moderate to sparse in abundance. Only two large bivalve borings were observed, cutting both metazoans and sediment.

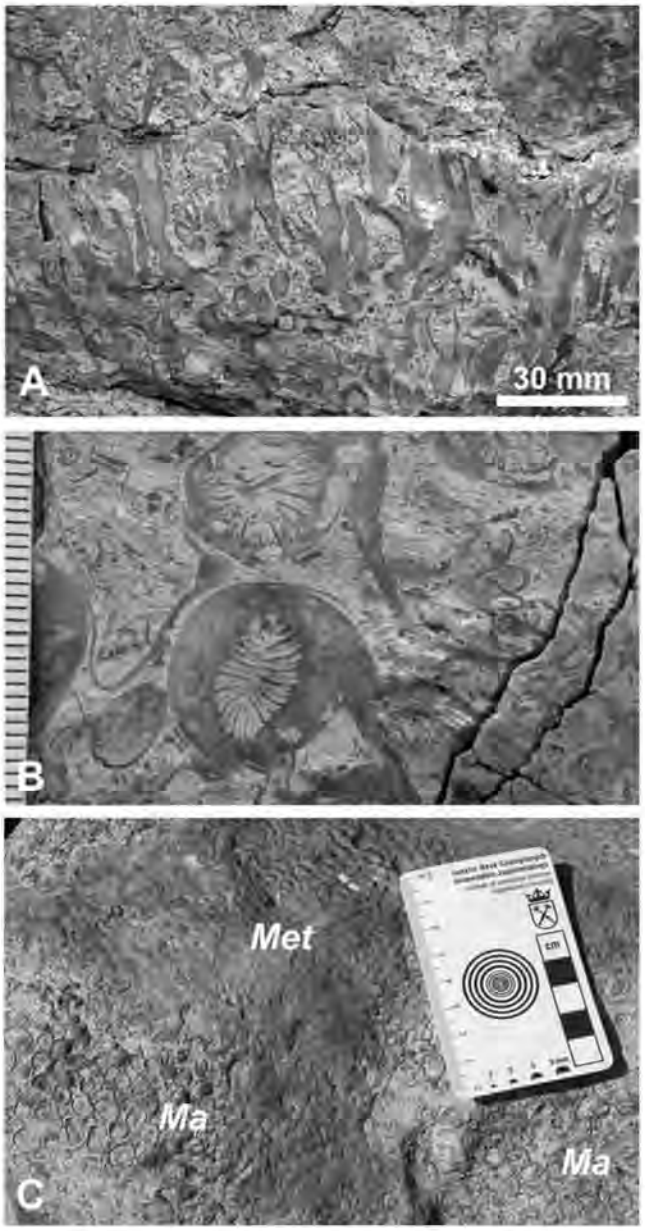


Fig. 5. Field photographs of pachythecaliine and *Mathesia*-bearing limestones from Vishovgrad Quarry (A, B) and Hotnitsa-ecotrack (C). **A** – *Pleurophyllia* sp. in growth position. Most coralites are in longitudinal section; note calcite spar cement filling most of interskeletal space, except uppermost part of coral branches. **B** – ?*Aulastrea* sp.; scale in millimeters. **C** – large massive colony of *Metaulastrea* sp. (*Met*) and densely clustered, small rudists *Mathesia darderi* (*Ma*)

PALAEOENVIRONMETAL INTERPRETATION

General interpretation of sedimentary setting at Rusalya

Analysis of section at Rusalya, about 42 m thick, allows placement of biostromes discussed within a broader sedimentary and environmental context. The dominance of bioclastic packstones, the sparse rudists, the occurrence of small corals, the presence of encrustations of *L. aggregatum*, "bacinellid" structures and the subordinate role of microbialites indicate that the lower part of the section (unit 1) represents the outer carbonate platform. Organisms and matrix sediment indicate a mildly mesotrophic environment and moderate hydrodynamics, but higher than during the development of the biostromes of unit 4 (see discussion below). Limestones, similar to those in unit 1, are common in the sedimentary succession of the Emen Formation at the Alexander Stambolijski Dam studied by Minkovska (1996) and by the present authors (unpublished data). Our studies of the section at the Alexander Stambolijski Dam revealed different facies, including limestones with corals, rudists, *L. aggregatum* and crusts with a "bacinellid" fabric. Pachythe-

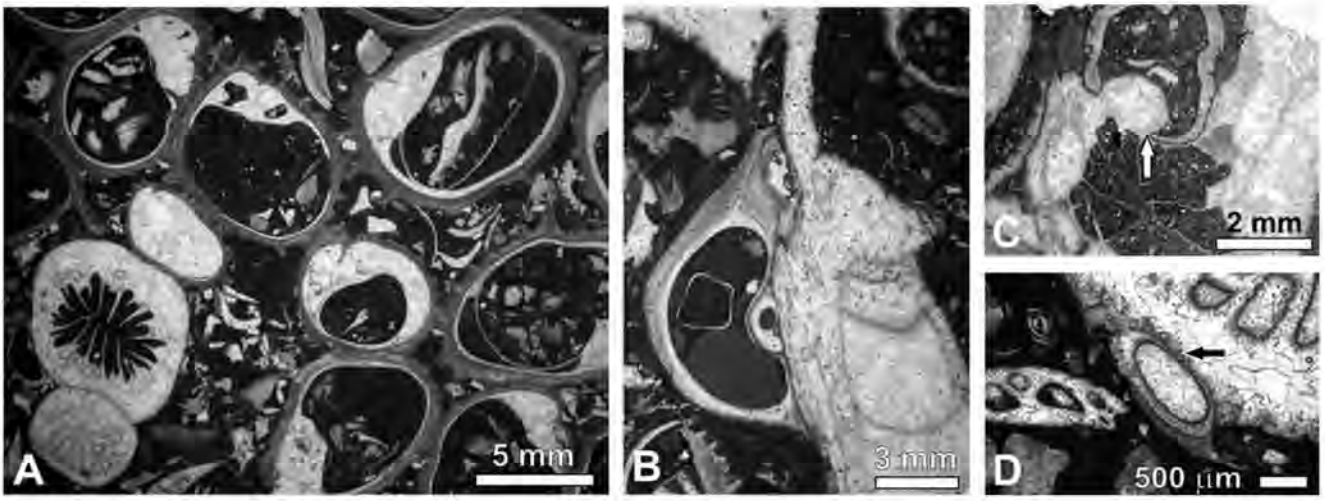


Fig. 6. Small rudist *Mathesia darderi* from pachythecaliine-rich boundstones. **A** – *M. darderi* aggregated in cluster and two branches of coral *Pleurophyllia* sp. **B** – rudist, attached to coral skeleton (longitudinal section). **C** – growth anomaly (arrow) of coral skeleton at boundary with rudist. **D** – juvenile rudist (arrow), closely attached to coral skeleton. Note two layers of rudist shell: inner layer originally aragonitic, and outer, calcitic layer. A – Vis 52/1, B – Ru 19-08/1, C – Ru, D – Vis 47/2

caliines, other branching corals and *Mathesia darderi* are absent there. Changes in lithology and biotic assemblages in units 2 and 3 and particularly the recurrent interlayers of rudist limestones, indicate changes in environmental parameters possibly controlled by changes of sea-level, but still remaining in the depositional setting of the outer carbonate platform.

It has been suggested previously that the pachythecaliine and *Mathesia*-rich biostromes studied (unit 4) developed in the distal portion of the rudist-dominated part of the carbonate platform (Kołodziej *et al.*, 2009; Fenerci-Masse *et al.*, 2011). In the topmost part of the section, biostromes of unit 5 built by dense rudist assemblages, cover directly the pachythecaliine-rich biostromes indicating an inner carbonate platform setting. Thus, the vertical, sedimentary and biotic succession in the section studied shows – with some fluctuations – a general shallowing trend, from the outer- to the inner-platform environment. Palaeoenvironmental inferences, based on an analysis of corals, rudists, microbialites and other biota from the pachythecaliine-bearing bioconstructions, are discussed below.

Corals

The coral communities in the bioconstructions discussed are dominated by phaceloid forms: pachythecaliines and less common *Calamophylliopsis* sp. In phaceloid corals, polyp tissue does not extend beyond the margin of the calice, so that such corals are considered pseudocolonies (Coates and Jackson, 1985; Roniewicz and Stolarski, 1999). Phaceloid corals were particularly well adapted to deal with high sedimentation rates in low-energy settings (e.g., Leinfelder *et al.*, 1994; Roniewicz and Stolarski, 1999; Dupraz and Strasser, 2002; Helm and Schülke, 2006). Geister (1995) calculated the growth rate of the Late Jurassic phaceloid *Aplosmilia* sp. as about 10 mm/year. However, a low rate of accumulation of allochtonous sediment is assumed for limestones discussed (but see discussion below on the growth rate of microbialites). A low energy environment at the transition from the inner to outer platform may be inferred, on the basis of the abundant, branching corals in the growth position (even though microbialite crusts enhanced the rigidity of the corals) and matrix-supported background sediment (mostly bioclastic wackestone).

Phaceloid, epithecate corals, with simple polyp organization, were highly developed in the Late Triassic and Late Jurassic (Roniewicz and Stolarski, 1999, and references therein). Modern, phaceloid corals are rare and epithecate, solitary corals occur in deep-water and cryptic habitats. Since the Late Cretaceous the decline of epithecate corals (including phaceloid ones), and the proliferation of non-epithecate corals are observed. This evolutionary trend probably was mainly driven by increased bioerosion in coral environments (Roniewicz and Stolarski, 1999).

It is worth emphasizing that corals, representing *Calamophylliopsis* (relatively common in the limestones studied) were described in the literature from various Jurassic–Cretaceous sediments , which implies growth under a different set of conditions, including stressful ones, such as higher sediment and nutrient input (for the Jurassic, see Leinfelder *et al.*, 1994; and references to systematic papers in Roniewicz, 1976; Turnšek, 1997; Morycowa, 2012; for the Cretaceous, see citation lists in Löser *et al.*, 2002). In the Barremian–Albian of Romania, *Calamophylliopsis* is known from pure limestones containing diverse corals associated with phototrophic and oligotrophic microencrusters, from '*Lithocodium–Bacinella*' facies, with poorly diversified corals, as well as from siliciclastic-dominated sequences (Kołodziej *et al.*, 2011a). It is also common in marls of the Lovech Urgonian Group (Idakieva and Ivanov, 2002; Idakieva, 2003).

During the Late Jurassic, the main period of development of phaceloid pachythecaliines (see the next chapter, the section Spatial and temporal proliferation of pachythecaliines), these corals (mostly amphiastraeids) occurred in different types of reef structures. They are known from coral-microbialite reefs, with photophilic/oligotrophic micro-

encrusters (e.g., Eliášová, 1975, 1981; Insalaco *et al.*, 1997; Kołodziej, 2003), and from coral thickets without microbial and/or the crusts mentioned above (e.g., Roniewicz, 1966; Insalaco *et al.*, 1997). Of particular significance is the common occurrence of specimens of phaceloid *Pleurophyllia*. Among Late Jurassic assemblages it was one of the most common, amphiastraeid corals, but except for in the Tithonian–Lower Berriasian Štramberk Limestone (see below), its record from the Lower Cretaceous is rare. In the list of citations on Cretaceous corals, Löser *et al.* (2002) mentioned only two species of *Pleurophyllia*, and sparse records worldwide.

A strictly actualistic approach to the palaeoecology of fossil corals cannot be applied, owing to evolutionary changes and the different, environmental preferences of many, modern reef corals (e.g., adaptation to high energy and an oligotrophic regime; see Wood, 1999). Coral communities from the biostromes studied are dominated by phaceloid forms. The question under debate is whether phaceloid corals were photosymbiotic or not. Some Late Triassic phaceloid corals (*Retiophyllia*, *Pachysolenia*) are considered to have been zooxanthellate, on the basis of stable isotope composition (Stanley and Swart, 1995). Studies of stable isotopes of the organic matrix from skeletons of the Upper Triassic solitary, pachythecaliine coral *Pachythecalis major*, recently performed by Muscatine *et al.* (2005), indicate that this species was photosymbiotic. The authors hypothesize that photosymbiosis may have played a role in scleractinian skeletogenesis, after the disappearance of the Rugosa in the Permian.

On the other hand, Recent, low-integrated or pseudocolonial corals are highly resistant to sedimentation and feed largely or entirely heterotrophically (Dryer and Logan, 1978, fide Sanders and Baron-Szabo, 2005 and Silvestri *et al.*, 2011). These observations have been used in the interpretation of fossil phaceloid corals. Kiessling *et al.* (2009) suggest that the occurrence of Early Jurrasic corals from southern France, mostly phaceloid forms, within siliciclastic sediments may indicate, that these possibly were mostly azooxanthellate. Thus, the unresolved question of whether phaceloid corals were zooxanthellate or not represents obstacle to the attempt to unravel the palaeoenvironmental parameters, controlling growth of the corals, studied here. However, rapid calcification does not always correlate with a zooxantellate status of corals (Marshall, 1996; Wood, 1999). Some branching azooxanthellate species, representing for example *Lophelia*, *Madrepora*, *Oculina* or *Tubastraea*, reveal a rapid growth rate, as much as 26 mm/year (Sabatier *et al.*, 2012, and references therein).

Phaceloid pachythecaliines were common and highly diversified during sedimentation of the Tithonian–Early Berriasian Štramberk Limestone from the Czech Republic (17 genera, 35 species) and Štramberk-type limestones from Poland (see next chapter, section Spatial and temporal proliferation of pachythecaliines). These reef limestones are characterized by the common occurrence of microbialites (typically laminated, with a micropeloidal microfabric), phototrophic microencrusters and diversified macrobiota (e.g., Morycowa, 1974; Eliášová, 1981; Eliáš and Eliášová, 1984; Kołodziej, 1997; Bucur *et al.*, 2005; for references see also Vašíček and Skupien, 2004). However, the factors that governed prolific growth and diversification of pachythecaliines during this time and at this part of the north Tethyan margin are unknown. Cuif and Stolarski (1999) have hypothesized that formation of the epithecal wall without septa (wall-based corals) in pachythecaliines and Recent *Gyunia* might be an adaptation to a stressful environment. However, in contrast to pachythecaliine corals from the Emen Formation, those from the Štramberk Limestone are associated with diversified corals and other biota, although short-term stressful events may be difficult to reveal.

Most of the Late Jurassic coral assemblages were described from the Upper Oxfordian and Kimmeridgian (Leinfelder *et al.*, 2002; Martin-Garin *et al.*, 2012). However, proliferation of pachythecaliines in the Tithonian was not strictly time controlled. By comparison, among 42 species from coral-bearing limestones of the Carpathian Foreland, comparable in age, only one belongs to Pachythecaliina (Morycowa, 2012). During that time, this area was located within a palaeolatitude position, similar to that of the carbonate platforms with sedimentation of the Štramberk Limestone. The possible reasons for environmental differences may be due to the fact that the former area was located slightly farther north, on the SW margin of the East European Craton, and was less affected by Late Jurassic/earliest Cretacous tectonics. In another example, in the Kimmeridgian to Valanginian, biostromal reefs (similar to the Štramberk Limestone, with regard to lithofacies; Ivanova *et al.*, 2008) in SW Bulgaria, Roniewicz (2008) recognized diversified coral communities (50 genera, 72 species), but only four genera and five pachythecaliine species.

Some cerioid/pseudocerioid amphiastraeids, such as *Amphiastrea*, were opportunistic organisms. The Middle–Late Jurassic *Amphiastrea piriformis* Gregory, 1900 is known from various lithologies/environments, including turbid, siliciclastic environments, with fluctuacting salinity. These corals were adapted to a high nutrient level and to the active removal of sediment (Fürsich *et al.*, 1994; Dupraz and Strasser, 2002). Similarly, cerioid/plocoid heterocoeniids are known from different sediments, including siliciclastics (e.g., Morycowa, 1964a; 1971; Beauvais, 1982; Morycowa *et al.*, 1994), implying broad, environmental adaptation.

By contrast to the Emen Formation in the study area, apart of the amphiastraeid *Metaulastrea*, *Amphiastrea* and heterocoeniid *Latusastrea*, other pachythecaliines are unknown within the diversified coral assemblages in marls and limestones of the Lovech Urgonian Group and Vraca Urgonian Group, as indicated by published results (see references in Geological setting and material), and the unpublished results of recent studies, including the analysis of a huge coral collection (coll. V. Zlatarski) housed at the National Museum of Natural History in Sofia.

Rudists

During the Cretaceous, corals coexisted with rudists in a range of environmental overlap. However, there is a general pattern in their distribution on the Urgonian and other Cretaceous carbonate platforms. Rudist associations charac-

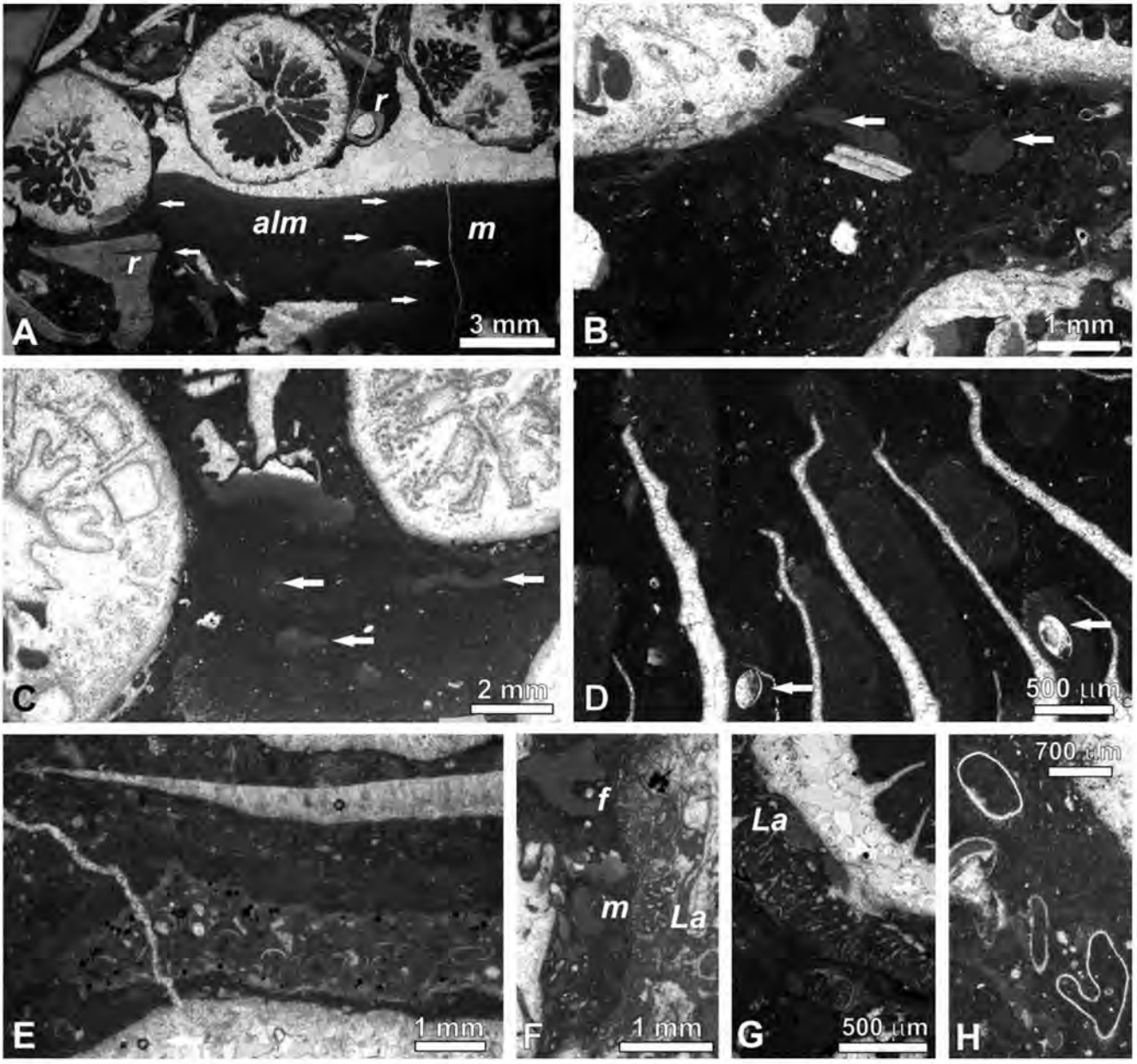


Fig. 7. Microbialites and some microfossils from pachythecaliine-*Mathesia*-microbialite boundstones. **A** – ?*Paracarolastraea* sp. and geopetally filled growth cavity. Arrows indicate boundary between automicrite (*m*) and allochtonous micrite (*alm*); *r* indicates rudists and their fragments. **B** – microbialites, poorly laminated locally, developed on and between coral branches; arrows show burrrowings or small growth cavities. **C** – small burrows (arrows) in microbialite, developed between coral branches. **D** – microbialite crusts on coral septa, mostly developed on their left side; arrows indicate ostracods. **E** – growth cavity within microbialites filled with ostracods and pyrite crystals. **F** – *Lithocodium aggregatum* (*La*), microbial crusts (*m*) and encrusting foraminifera (*f*). **G** – coral, encrusted by *Lithocodium aggregatum* (*La*). **H** – hyaline foraminifer, exhibiting fine spines (?*Ramulina* sp.) within microbialites. A – Vis 40/1, B – Ru 34/3, C – Ru 22/2, D – Vis 2/3, E – Ru 14-08/2, B – Ru 34/3, G – Ru 30-09, H – Ru 9-10

terized different settings, depending on morphotype, but occurred mainly in the inner carbonate platform environment; bioclastic limestones are referable to the outer platform, while coral facies to the transition between the inner and outer platform. The biotic distribution pattern was largely controlled by changes in environmental conditions, forced by external factors, such as water turbidity, nutrient level and hydrodynamic regime (e.g., Masse and Philip, 1981; Gili *et al.*, 1995a, b; Skelton *et al.*, 1997). In the mixed, carbonate-siliciclastic Urgonian, system in Bulgaria, rudists (poorly known in contrast to corals) may co-occur with corals, but usually they occur in separate lithosomes. Moreover, rudists are absent in the marls, while corals may be highly diversified there.

Apart from the limestones discussed, *Mathesia darderi* is unknown from other deposits of the Urgonian complex in Bulgaria. *M. darderi* is included in the rudist family Monopleuridae that, in general, played a limited role on the Early

Cretaceous carbonate platforms of the Mediterranean region. Locally, however, monopleurids were abundant and may have a significant, constructional potential, especially during the Early Valanginian and Late Aptian–Albian, with *M. darderi* as a key species. Relatively thick lithosomes (up to 3 m) are usually formed by dense, monospecific assemblages (Fenerci-Masse, 2006 fide Masse and Fenerci-Masse, 2010; Fenerci-Masse *et al.*, 2011; Skelton and Gili, 2012).

The monospecific genus *Mathesia* is known from the Late Barremian to Middle Albian. The first Late Barremian occurrences have recently been recognized in Bulgaria and Spain. During the Late Barremian to Early Aptian, this genus was present only locally and later was widespread (Fenerci-Masse *et al.*, 2011) escaping the mid-Aptian crisis, when 90% of species and 70% of the Mediterranean rudist genera disappeared (Masse, 1989; Skelton and Gili, 2012). The ecological changes, recorded in *Mathesia* through time, reflect a displacement from the distal, rudist-dominated part to the proximal part of carbonate platforms (Fenerci-Masse *et al.*, 2011). In the Albian of southern Spain, *M. darderi* build dense, monospecific assemblages, found interbedded with intertidal stromatolites and muddy sediments (Fenerci-Masse, 2006; see Fenerci-Masse *et al.*, 2011). In SE Spain, *M. darderi* occurs within the uppermost Barremian rudist-rich (Requieniidae, Monopleuridae) packstones and wackestones, with dasycladalean algae, above marls and dasycladd-rich limestones and below lower Aptian orbitolinid-rich marly limestones with quartz (Fenerci-Masse *et al.*, 2011). Thus, with regard to the sedimentary context, including biofacies (lack of corals), this occurrence differs from the *Mathesia*-bearing limestones of the Emen Formation in Bulgaria.

Rudists that are in contact with corals were attached to the skeleton of phaceloid corals, which, unlike branching ramose forms (like recent *Acropora*), were not covered by living tissue (except for the tips of branches). Growth anomalies, observed both in corals and in rudists, are very rare, and suggest rare, direct tissue contact (*in vivo* interaction). However, some kind of synecological relationship between rudists and corals is plausible. Synecological interactions in coral-rudist associations, such as the one from the Campanian of Spain (Götz, 2003), have been described only rarely in the literature. Protuberances of rudist shells were explained by Götz (2003) as possible defence reactions of the rudist against the coral cnidia. However, both groups might have benefited from this coexistence. Rudists might provide hard substrates for coral settlement, while rudists were stabilised by encrusting corals (Götz, 2003). A similar relationship may be assumed for the coral-rudist association studied, even though indications for *in vivo* association are only hypothetical.

Physical erosion during the growth of corals and rudists was rather negligible, because of the inferred, low energy level. Common, small rudist fragments are rather a result of intrinsic (shell structure/mineralogy), than extrinsic (hydrodynamics, bioerosion), taphonomical factors. Fragmentation of rudists, due to their composition, that is aragonite (originally) inner and calcitic outer shell layers, may be an important, synsedimentary modifier of the original rudist biocoenosis (Sanders, 1999).

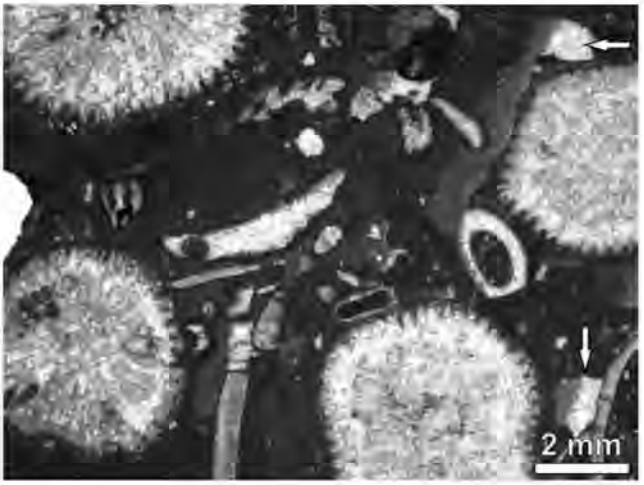


Fig. 8. *Calamophylliopsis* sp. Arrows indicate geopetally filled growth cavities or small burrows. ZPAL Bulg 1/1

Other macrobiota

In general, apart from pachythecaliine corals and *M. darderi*, macrobiota and their remains are not common in the bioconstructions studied. Therefore, small gastropods are of special interest, as they are common components of the biocoenosis described. Taxonomy and feeding behaviour of these gastropods are unknown. They were possibly grazers or sediment feeders, basing on assumed abundant, organic matter in the microbialites. An increased nutrient level may also enhance primary production of fleshy algae, favouring herbivorous gastropods (see Dupraz and Strasser, 2002).

Microbialites

A characteristic feature of the bioconstructions analysed are dense, nearly always non-laminated, micritic crusts, occurring on and between skeletal metazoans, as well as within semi-closed microcavities. Their genesis may have inferences for the environmental interpretation of the depositional environment. These crusts are called here *microbialites*, the term used in a broad meaning, i.e. as a result of organomineralization *s.l.*, defined as microbially-induced and microbially-influenced mineralization (Dupraz *et al.*, 2009). Automicrite is a more inclusive term and can be applied both for 'classical', microbial fabrics, as well as for microcrystalline carbonates, which originated in association with non-living organic macromolecules, that is related to organomineralization *s.s.* (Trichet and Défarge, 1995). Some authors propose use of the term *automicrite* instead of *microbialite*, if the origin of autochtonous micrite is unknown (e.g., Reitner and Neuweiler, 1995; Bourque, 1997; Neuweiler *et al.*, 1999; Webb, 2001; Schlager, 2003). Automicrite that resulted from organomineralization *s.s.* was recognized by Neuweiler *et al.* (1999) in exceptionally well preserved, organic fractions in the Albian carbonate mud mounds of Spain. According to these authors, the Late Jurassic represents an important period of organomineralization *s.s.* and resulted in the precipitation of automicrite, which is frequently referred to as micro-

bial crusts, common in coral- and sponge-microbialite reefs (e.g., Leinfelder *et al.*, 1993, 1994; Leinfelder, 2001; Dupraz and Strasser, 2002; Olivier *et al.*, 2004; Matyszkiewicz *et al.*, 2012; Pleş *et al.*, 2013). Discrimination between these different processes and products in fossil material is a challenge for future research (Riding, 2000).

Attribution of microbialites from the Emen Formation to one of the major categories of stromatolites, thrombolites, dendrolites, or leiolites can not be strictly applicable here. These categories are based on macrofabrics, namely laminated, clotted, dendritic and aphanitic respectively (Kennard and James 1986; Schmid, 1996; Riding, 2000), which are not recognizable macroscopically in the material studied. These main categories are also used in the classification of microbialites, based on a combination of macrostructure and microstructure (Schmid, 1996; Flügel, 2010, fig. 9.1B). In such an approach, microbialite crusts in the biostromes studied can be classified largely as leiolite microbialites, i.e., microbialites with dense microstructure.

The presence, mostly on coral branches, of differentially preserved non-rigid and calcified sponges raises the question of possible contribution of non-rigid sponges to microbialite formation. Sponge spicules, occurring locally within microbialites, reticulate microfabric, similar to sponge structures recognized in Triassic sponge-microbial stromatolites (Szulc, 1997, 2000, fig. 21g), as well as a lateral transition from well preserved sponge to micritic/micropeloidal microfabric, indicate that some microbialites might be the result of sponge soft-tissue diagenesis. Microbially induced carbonate precipitation (microbialite formation) inside decaying Recent and fossil sponge tissue is well documented (e.g., Reitner, 1993; Reitner and Neuweiler, 1995; Delecat and Reitner, 2005; Reolid, 2007). Increased alkalinity induces dissolution of siliceous spicules and may be responsible for the lack of microscleres in some facies (Delecat and Reitner, 2005).

Foraminifera, occurring within microbialites may be an additional argument in the discussion of the possible contribution of sponges to microbialite formation. They are similar to those reported from fossil and modern sponge meshworks (e.g., Guilbault *et al.*, 2006; Reolid, 2007) or inhabiting cavities (e.g., Helm, 2005; Helm and Schülke, 2006, fig. 11l; Schlagintweit and Velić, 2012, fig. 7g, h). Alternatively, these foraminifera may be interpreted as loosely attached to microbialite crusts. Automicrite occurs locally between coral skeletal elements, thus indicating development of microbialites also in aphotic conditions (compare Albian microbialites: Neuweiler, 1993, 1995). Apart from the calcification of decaying sponges (sponge 'container automicrites'), these organisms, as well as the soft tissue of other metazoans may be primary sources of organic material (Reitner and Neuweiler, 1995; Neuweiler *et al.* 1999).

Micropeloids, which are rare in the limestones studied, may be similar in origin to the dense microbialite crusts. Many authors regard peloids as *in situ* growth products, related to randomly distributed nucleation centers, or as a result of bacterial degradation of organic matter (e.g., Reid, 1987; Neuweiler, 1993; Riding and Tomás, 2006, and references therein).

Bryozoans, serpulids, rare *L. aggregatum* and 'bacinellid' crusts, sporadically red algae and juvenile rudists directly encrust corals or rudists. Except some foraminifera of uncertain mode of attachment and generic status, discussed above, microbialites are never encrusted by microencrusters. That suggests that they were only partially lithified and hard substrate was not available for larval settlement. Such an interpretation is supported by the lack of borings in microbialites (except for rare, large bivalve borings in metazoans, microbialites and sediment matrix). Similarly, a lack of metazoan encrusters on microbialites was observed by Webb (1999) in Carboniferous patch reefs, and by Neuweiler (1993) in Albian microbialites. According to Webb (1999), this implies that some automicrites (= microbialites *s.l.*) have not been lithified at the sediment-water interface, but were formed as synsedimentary precipitates within sediment. The presence of burrows also indicates that the studied microbialites were not rigid, but only semi-consolidated, when burrowing took place (cf. Riding, 2000; Riding and Tomás, 2006). In contrast to these examples, intergrowths of skeletal microencrusters and microbialites were recorded for example in the Late Jurassic reefs, indicating the presence of a hard substrate and interruptions of microbialite growth (Olivier *et al.*, 2003). Growth cavities in the material studied are small; their presence is marked by geopetal fillings and cryptic ostracods (cf. Aubrecht *et al.*, 2002; Shen and Webb, 2005).

In Recent reefs, enhanced microbialite growth is characteristic for environments with higher nutrient levels and elevated alkalinity (Camoin and Montaggioni, 1994; Camoin *et al.*, 1999, 2006; Sprachta *et al.*, 2001), which is also accepted for fossil coral reefs (e.g., Leinfelder *et al.*, 1994; Dupraz and Strasser, 2002; Olivier *et al.*, 2004). Sedimentation of allochthonous deposits and microbialite growth rate, in relation to the growth of metazoan constructors, is crucial for the development of a constratal or superstratal growth fabric, which has architectural, palaeoecological, sedimentological and diagenetic implications (Insalaco, 1998). Microbialite growth is favoured by a low accumulation rate, but the growth rate is difficult to estimate, because there are no modern analogues for fossil, reefal microbialites. Microbialites from cryptic caves of Lizard Island display very low net growth rates of 10 to 15 mm/1000 years (Reitner, 1993). However, in shallow-water reefs, where corals are closely intergrown with microbialites, they might have grown as fast as the corals, about 1–2 mm/year, as postulated by some authors (see Schmid, 1996; Schmid *et al.*, 2001). Seard *et al.* (2011) observed microbialite growth rates, ranging from 7 to 12 mm/year. Such unusually rapid growth rates probably result from their development during a period of environmental change (sea-level rise), while in more stable environments, they are significantly lower (Seard *et al.*, 2011; Heindel *et al.*, 2012).

As discussed above, phaceloid corals were well adapted to high sedimentation rates, soft, muddy substrates and low-hydrodynamic regimes. A low background sedimentation rate is assumed for the biostrome formation analysed. However, the growth of phaceloid corals also might be favoured by a higher growth rate of microbialites. However, it was not a dominant influence on the development of phaceloid corals, becuase except for *Calamophylliopsis* (suborder Faviina), only phaceloid pachythecaliines were recog-

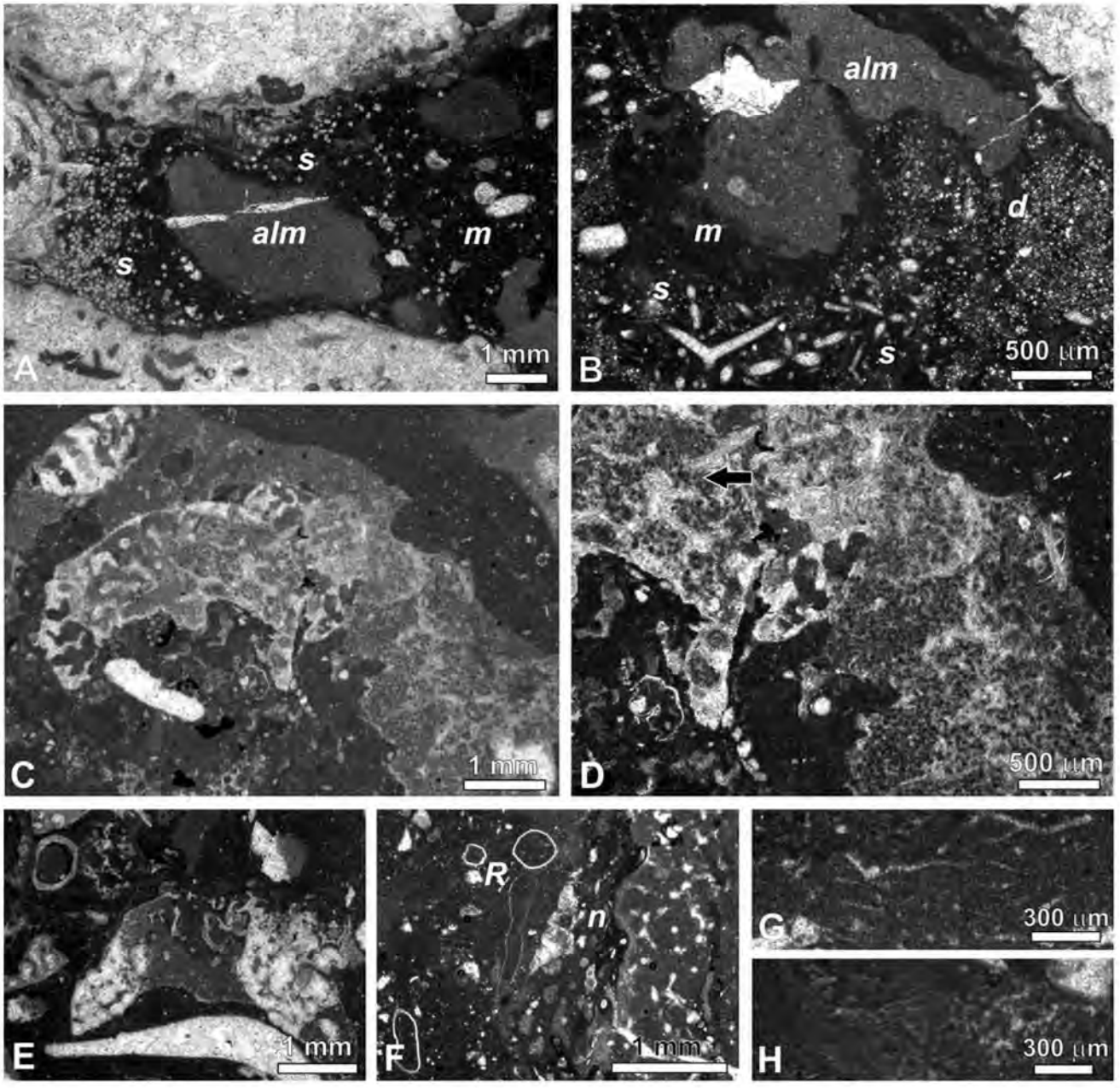


Fig. 9. Differential preservation of sponges from pachythecaliine-*Mathesia*-microbialite boundstones **A, B** – sponge spicules (s) within dark-coloured microbialites (*m*); *alm* allochtonous micrite, filling small growth cavities; d (in B) indicate dolomite crystals within microbialites (compare Fig. 15F). **C–E** – differential preservation of rigid (calcified) sponges. Micropeloids in C and D, possibly resulted from degradation of sponge tissue. Note micropeloids in intraskeletal space (arrow in D). **F** – non-rigid sponge, encrusted by nubeculariid foraminifera (*n*) and microbialites with *Ramulina*-like foraminifera (*R*). **G** – reticulate microfabric, and **H** – needle-like structures, possibly resulted from dissolution of sponge spicules. A – Vis 2/3, B –Vis 2, C, D – Ru 7257/1, E – Ru 34/3, F – Vis 47/2, G, H – Zar 996/3

nized. If coral accretion occurred at a rate, similar to that of microbialite growth, then limited, positive relief, that is, a constratal coral growth fabric (*sensu* Insalaco, 1998) may be inferred.

Dolomite crystals, recognized in the samples from Vishovgrad, possibly are restricted to microbialites, which indicates the syngenetic nature of dolomite formation and a possible link with microbial activity or organomineralization *s.s.* (cf. Wright and Wacey, 2005; Mastandrea *et al.*, 2006; Bontognali *et al.*, 2010).

At elevated nutrient levels, bioerosion generally is considered to be enhanced (Hallock, 1988; and Sanders and Baron-Szabo, 2005 for review). However, increased bioerosion is not observed in the material studied. Macroborings in metazoan skeletons are moderate or scarce, and absent in microbialites. A higher nutrient level, constant or episodic, raises the question about water oxygenation. Episodes of low oxygen concentrations are generally invoked to explain microbialite development in Late Jurassic reefs (Leinfelder *et al.*, 1994; Betzler *et al.*, 2007). However, in the material

studied here, the fauna, although not highly diversified, does not support the concept of a poorly oxygenated bottom. Moreover, some Jurassic microbialites could have formed in oxic waters (Olivier and Boyet, 2006; Olivier *et al.*, 2011).

Lithocodium/Bacinella

Lithocodium aggregatum and associated, microbial structures, with a 'bacinellid' fabric ("*Bacinella irregularis*") are an important issue in palaeoenvironmental interpretation of Upper Jurassic and Lower Cretaceous shallow water limestones. Difficulties in the interpretation of depositional environment are due to their unclear, systematic position and environmental demands. *Lithocodium aggregatum* Elliot, 1956 was variously interpreted, among others as algae, calcimicrobes or encrusting foraminifera, while *Bacinella irregularis* Radoičić, 1959 was mostly interpreted as microbial structures. Some authors assumed that both taxa represent different parts of one organism (for review see Schmid and Leinfelder, 1996; Rameil *et al.*, 2010; Schlagintweit *et al.*, 2010; Schlagintweit and Bover-Arnal, 2012, 2013). Recently, new interpretations have been proposed for taxa, traditionally labelled as *L. aggregatum* and *B. irregularis*. Schlagintweit *et al.* (2010) and Schlagintweit and Bover-Arnal (2013), based on studies of Aptian material, interpreted *L. aggregatum* as ulvophycean green alga with heterotrichale encrusting thallus, and *B. irregularis* as an euendolithic chlorophycean alga. Most of structures described as *B. irregularis* are, according to these authors, vesicular, microbial crusts with "bacinellid" fabrics. *L. aggregatum* may develop also a cryptic stage with net-like structure (Schlagintweit and Bover-Arnal, 2012) which can be misinterpreted with "bacinellid" structures. Most of the structures described as *B. irregularis* are, according to these authors, vesicular, microbial crusts with "bacinellid" fabrics. *L. aggregatum* may develop also a cryptic stage with a net-like structure (Schlagintweit and Bover-Arnal, 2012), which can be misinterpreted as "bacinellid" structures. For a summarizing diagram, showing different, morphological and taxonomic interpretations, see Huck *et al.* (2012, fig. 8). Further interpretative complications arise, because many crusts (in particular in the Upper Triassic and Upper Jurassic rocks), determined in the literature as *L. aggregatum*, are in fact sponge borings in microbialites or other carbonate substrates (Cherchi and Schroeder, 2010, 2013; Schlagintweit, 2010).

Occurrences of *L. aggregatum s.s.*, *Lithocodium*-like entobian borings and "bacinellid" structures in the Late Jurassic–earliest Creataceous, coral-microbialite reefs are commonly interpreted as an indicator of shallow-water, although data from the literature indicate that *L. aggregatum s.s.* was adapted also to outer-shelf/ramp environments (see discussion in Bover-Arnal *et al.*, 2011; Schlagintweit and Bover-Arnal, 2012; Huck *et al.*, 2012). These microencrusters are also assumed to be an indicator of oligotrophic or mildly mesotrophic, reefal and lagoonal environments (e.g., Leinfelder *et al.*, 1993; Dupraz and Strasser, 2002; Olivier *et al.*, 2004; Ivanova *et al.*, 2008). However such an interpretation seems to be appropriate, only when they are associated with other microencrusters and occur as subordinate components in Late Jurassic–Early Cretaceous coral reefs and lagoonal facies (e.g., Rameil *et al.*, 2010). During the mid-Cretaceous time, in particular in the Early Aptian, a local "bloom" of so-called "*Lithocodium-Bacinella*" facies (a descriptive term) occurred (Immenhauser *et al.*, 2005; Huck *et al.*, 2010). It is assumed that the Aptian "*Lithocodium-Bacinella*" facies show a more complex, biotic pattern, controlled by fluctuating nutrient levels, sea-water alkalinity, elevated seawater temperatures, seawater acidification and low sedimentation rates, superimposed on global perturbations of neritic ecosystems (Neuweiler and Reitner, 1992; Immenhauser *et al.*, 2005; Huck *et al.*, 2010; Rameil *et al.*, 2010; Bover-Arnal *et al.*, 2011; Huck *et al.*, 2012).

In the pachythecalline-bearing limestones studied, corals and other metazoans are rarely encrusted by *L. aggregatum* and "bacinellid" structures, but instead they are mostly encrusted directly by microbialites or by heterotrophic microorganisms and small rudists, followed by microbial crusts. The studies of Late Jurassic coral reefs revealed that the lack of phototrophic-dominated organisms in the first layer of encrustation indicates more turbid waters and/or a higher nutrient level (Leinfelder *et al.*, 1993; Dupraz and Strasser, 2002; Olivier *et al.*, 2004; Helm and Schülke, 2006). Similar, environmental controls can be assumed for the Early Cretaceous coral reefs, which in contrast to the Late Jurassic reefs, are studied less extensively in this respect. Even though the taxonomic interpretation of some structures, described as *L. aggregatum* and *B. irregularis* (= "bacinellid" structures), have been recently re-interpreted, the environmental inferences appear to be still valid, when these organisms occur as a moderate component of coral reefs, and not as a dominant bioconstructor, as in some Aptian occurrences. However, as concluded by Schlagintweit *et al.* (2010, p. 541), "...the paleoenvironmental significance of *Lithocodium aggregatum* occurrences must be carefully viewed in each case study".

Concluding remarks

The unique association of pachythecaliines and *Mathesia* forming biostromes occurs within a palaeogeographically limited area. The resulting bioconstructions (biostromes and possibly also low-relief bioherms), unknown elsewhere, imply particular environmental factors driving their growth and microbialite formation. *Lithocodium* and 'bacinellid' structures are moderately common in unit 1 at Rusalya. Obviously the shift from the outer carbonate platform (unit 1) towards the more inner platform setting (unit 4) has lead to the change of environmental factors, such as lowering of the hydrodynamic regime and possibly increasing nutrient level. These changes favoured growth of phaceloid pachythecaliine corals, nearly monospecific rudist assemblage (*Mathesia darderi*), facilitated growth of microbialites, but limited growth of *L. aggregatum* and "bacinellid" structures. Difficulties in deciphering environmental constraints are, among other factors, due to the lack of comparable, fossil biocoenoses. *Mathesia* up to now was known from deposits lacking, or with rare corals. Phaceloid pachy-

thecaliines were rare in the Early Cretaceous, whereas Late Jurassic taxa were relatively common, but occurred in various, sedimentary settings, as indicated by host lithology and associated biota. By comparison with the corals studied, highly diversified, phaceloid pachythecaliines, known from the Tithonian–Lower Berriasian Štramberk Limestone and Štramberk-type limestones (Czech Republic, Poland), are associated with diversified corals and other biota, including phototrophic/oligotrophic microorganims.

In the best exposed section at Rusalya, the pachythecaliine-rich biostromes attain only a thickness of about 2.5 m. Thus, it is tempting to view development of this biofacies during a short time interval and as a potential, local, stratigraphic marker. However, stratigraphic data from Hotnitsa and limited sampling in Hotnitsa and Zarapovo do not permit unambiguous, stratigraphic implications. However, development of this biofacies appears to have occured largely during the middle Late Barremian.

GENERAL REMARKS ON MORPHOLOGY, SYSTEMATICS AND DISTRIBUTION OF PACHYTHECALIINA

Morphology and microstructure

The suborder Pachythecaliina Eliášová, 1976, in particular the Late Triassic family Zardinophyllidae Montanaro Gallitelli, 1975 (= Pachythecaliidae Cuif, 1975), and the Jurassic–Cretaceous Amphiastraeidae Alloiteau, 1952, contains skeletal features non-typical for scleractinian corals: a thick wall (pachytheca), and septa, commonly deep in the calice and arranged in bilateral symmetry (quasi-radial in the adult stage of some taxa). Pachythecallines, except most heterocoeniids, are solitary or their skeleton indicates polyps that originally were poorly integrated. They are mostly of the phaceloid, cerioid or pseudocerioid growth form. Amphiastraeids, the most common pachythecaliines (Roniewicz and Stolarski, 2001; Stolarski and Russo, 2001), reproduced asexually, by unique Taschenknospung ('pocket'-budding). Other families, classified into Pachythecaliina, share only some features with their supposed relatives, the zardinophyllids (Montanaro Gallitelli, 1975; Cuif, 1975, 1981) and amphiastraeids (Eliášová, 1975, 1976b, 1978; Melnikova and Roniewicz, 1976; Kołodziej, 1995, 2003; Roniewicz and Stolarski, 2001; Stolarski and Russo, 2001; see also Amphiastraeina and Heterocoeniina, generally characterized in Baron-Szabo, 2002; Löser, 2009; and http://www.corallosphere.org).

The skeleton microstructure has been debated focussing on trabecular *versus* non-trabecular microstructure of septa and wall. Most post-Triassic pachythecaliines have badly preserved skeletons and diagnostic microstructural characters are not well recognized. The dominant view is that the wall (pachytheca) is built by horizontal modules with circumferential calcification centers (Cuif, 1975; Roniewicz and Stolarski, 2001; Stolarski, 2003; Cuif, 2010). Change in the style of biomineralization, from horizontal modules, having circumferential calcification centres, to a strictly trabecular one (vertical trabeculae, with axially arranged calcification centers) was observed in the Upper Triassic amphiastraeid *Quenstedtiphyllia fritschi* (Volz, 1896) (see Roniewicz and Stolarski, 2001). Septal microstructures of pachythecaliines *s.s.* were considered both as non-trabecular (Cuif, 1975, 2010; see also Stolarski, 2003), and minitrabecular (see discussion in Kołodziej, 1995; Roniewicz and Stolarski, 2001). Roniewicz *et al.* (2007, p. 593) defined the microstructure of Triassic pachythecaliines as "Wall epithecal, thick and modular in structure; septa thin and built of centripetally growing trabeculae, or septal microstructure fibronormal (in relation to the midseptal plane); septal faces not ornamented". However, if we take into account also pachythecaliines *s.l.* (*sensu* Stolarski and Russo, 2001), not all post-Triassic pachythecaliines, particularly heterocoeniids do fit with such definition. Wall can be thin (e.g., *Donacosmilia*), and in contrast to the zardinophyllids, even in amphiastraeids, septal faces can show ornamentation (e.g., Fig. 16D, E). Differences in microstructures between amphiastaeids and heterocoeniids are discussed below. Moreover, traditional terminology dealing with skeletal microstructure (thick-trabecular, minitrabecular; Roniewicz and Morycowa, 1993), possibly requires modification, owing to the new model of skeletal coral growth, proposed by Stolarski (2003).

The microstructure of the wall and septa in post-Triassic pachythecaliines has been interpreted variously. In Jurassic–Cretaceous amphiastraeids, the wall is built up of "...well arranged modules of the shape of horizontal spines" (Roniewicz and Stolarski, 1999, pp. 144–145; see also Ogilvie, 1897; Morycowa, 1964b; Eliášová, 1975; Kołodziej, 1995; Roniewicz and Stolarski, 2001). The pachytheca – a wall diagnostic for Pachythecaliina – implies that it is built by fibrous microstructure. In fact, in most pachythecaliines, the microstructure of the septa and wall is unknown, owing to the poor state of preservation. Moreover, differentiation in diagenetic alterations of the wall in amphiastraeids and related families might suggest an original variability in microstructure (Eliášová, 1976b; Roniewicz and Stolarski, 1999; Kołodziej, 2003). A wall in pachythecaliines (including heterocoeniids) is commonly termed as "wall developed in advance to septa" (Cuif, 1975, 2010; Cuif and Stolarski, 1999; Roniewicz and Stolarski, 2001; Stolarski and Russo, 2001) or "wall developed prior to septa" (see Kołodziej, 1995).

In particular, there is a controversy, concerning the microstructure of heterocoeniid skeletons, which was interpreted in different ways. Septa have been described as built by large trabeculae (Morycowa, 1971; Roniewicz and Morycowa, 1993) or minitrabeculae (Kołodziej, 1995). It is worth emphasizing that septa in heterocoeniids (even the primary septum) can be thinner than the lower limit of thick trabeculae. The diameter of thick trabeculae *sensu* Roniewicz and Morycowa (1993, p. 235) is "...over 50 μm (usually more than 100 μm) to ca. 300 μm". Moreover, there are indications suggesting that the modular structures of amphiastraeid *Amphiastrea* and heterocoeniid *Latusastrea* are similar (Kołodziej, 1995). Important difference between these two groups is a trabecular(?) microstructure of a peritheca, a skeletal structure, occurring in some heterocoeniids, but unknown in other pachythecaliines. Relics of

more diverse, than usually thought, septal and wall microstructures were observed in some pachythecaliines *s.l.* (Eliášová, 1976b; Kołodziej, 2003, figs 3, 4).

Classification and phylogeny

Following Roniewicz and Stolarski (2001), some authors distinguish the suborder Pachythecaliina instead of the suborder Amphiastraeina (Stolarski and Roniewicz, 2001; Stolarski and Russo, 2001; Kołodziej, 2003; Roniewicz, 2008; Melnikova and Roniewicz, 2012; Morycowa, 2012). Others still accept the priority of Amphiastraeina. However, the possible relationships of Triassic pachythecaliines with amphiastraeids and related families are seldom discussed by these authors (e.g., Baron-Szabo, 2002, 2006; Turnšek *et al.*, 2003; Löser, 2008c, 2012; Löser *et al.*, 2009).

Usually the following families are included in the Pachythecaliina (= Amphiastraeina): (1) the Late Triassic Zardinophyllidae (recent finding also in the Lower Jurassic; Melnikova, 1975; Melnikova and Roniewicz, 2012), and Late Triassic–Cretaceous (2) Amphiastraeidae [two amphiastraeid genera *Quenstedtiphyllia* Melnikova, 1976 and *Sichuanophyllia* Deng Zhanqiu et Zhang Yansheng, 1984 (= *Lubowastraea* Melnikova, 1986) are known from the Upper Triassic], and Jurassic–Cretaceous (3) Carolastraeidae Eliášová, 1975, (4) Donacosmiliidae Krasnov, 1970, and (5) Intersmiliidae Melnikova et Roniewicz, 1975. More problematic is the systematic position of the family Heterocoeniidae Oppenheim, 1930, which is usually classified in the separate suborder Heterocoeniina Beauvais, 1977. Previously heterocoeniids were classified in different suborders; some heterocoeniids were classified within the Amphiastraeidae (Vaughan and Wells, 1943; Wells, 1956; see Kołodziej, 1995). L. Beauvais (1974, 1976) believed that there are similarities (also in microstructure) between Amphiastraeidae and Heterocoeniidae and later L. Beauvais (1981) classified Amphiastraeidae together with Heterocoeniidae in a new suborder Distichophyliina, a suborder not recognized in current coral classifications. By contrast, M. Beauvais (1977, 1982) included Heterocoeniidae in the new suborder Heterocoeniina. Eliášová (1976b) accepted both Amphiastraeina and Heterocoeniina. However, she classified them together with the new suborder Carolastraeina (not recognized in current coral classifications), and Triassic Pachythecaliina in the separate order Hexanthiniaria (see below). Hence, she assumed morphological similarities and phylogenetic relationships for these coral groups. Kołodziej (1995) proposed to include Heterocoeniidae (superfamily Heterocoenioidea) in Amphiastraeina, and later into Pachythecaliina (Kołodziej, 2003), a view, which is also held in the present account. Stolarski and Russo (2001) considered heterocoeniids as "supposed pachythecaliines". Baron-Szabo first classified heterocoeniids into Heterocoeniina (e.g., Baron-Szabo and Steuber, 1996; Baron-Szabo, 1998), later into Amphiastraeina (Baron-Szabo, 2002, 2006). Taxonomical difficulities, concerning heterocoeniids, are well exemplified by *Latusastrea* Orbigny, 1849, a genus, which between 1940–1990 was classified within five suborders (Turnšek and Löser, 1989). The suborder Heterocoeniina was accepted recently in scleractinian systematics by Morycowa and Marcopoulou-Diacantoni (2002), Idakieva (2003), Morycowa and Decrouez (2006), Roniewicz (2008), and by Löser (e.g., 2008a, b, c, 2009, 2010).

Co-occurrence (in the limestones studied) of pachythecaliines *s.s.* (*sensu* Stolarski and Russo, 2001), that is, amphiastraeids (five genera, six species), and pachythecaliines *s.l.*, that is, carolastraeids (one genus, two species), intersmiliids (one genus, one species), donacosmiliids (one genus, one species), and heterocoeniids (four genera, four species), indicates similar environmental preferences. The occurrence of four heterocoeniid genera, displaying the phaceloid growth form, which is rare in this family, should be emphasized. The co-occurrence with other four pachythecalline families is not conclusive evidence of phylogenetic relationships; however, it is one more piece of evidence, supporting such an interpretation. A similar co-occurence of five pachythecaliine families is known from the Tithonian–Lower Berriasian Štramberk Limestone (Czech Republic) and its equivalent in the Polish Outer Carpathians. Only heterocoeniids are rare there, but in general they were rare and poorly diversified in the Jurassic and the earliest Cretaceous. Certainly, taxonomic variability of pachythecaliines in the limestones studied is higher, as some of findings were not described here, owing to a poor state of preservation or not enough, available thin sections. Further sampling in the active quarry at Rusalya should provide more data on these unique anthozoans during their Cretaceous acme.

Taschenknospung, a peculiar type of budding, is only well recognized in amphiastraeids. Possibly it occurs also in some heterocoeniids, as indicated by the relationship of parent and daugther corallites in *Thecidiosmilia morycowae* (see Kołodziej, 1995). On the other hand, strongly developed, lateral, septal ornamentation or even septal outgrowths are an important feature of heterocoeniids, but only for some genera, while others can have septa with poor ornamentation. In *Heterosmilia* gen. nov., a heterocoeniid genus established in this paper, only the primary septum has strong, septal outgrowths, while other septa lack ornamentation. Strong, septal outgrowths are not common in scleractinians, but occur also in other coral groups (e.g., Morycowa, 1971; Stolarski *et al.*, 2004), including Rhipidogyrina, which have true, aphophysal septa (Eliášová, 1973).

In summary, intersmiliids, carolastraeids, donacosmiliids and heterocoeniids are "...much easier clustered with pachythecaliines than with other coeval scleractinians" (Stolarski and Russo, 2001, p. 253), even taking into account microstructural differences. In particular, some heterocoeniid genera are morphologically closer to amphiastraeids than to end members of a spectrum of Heterocoeniidae. Heterocoeniids include some colonial genera with high integration level, which distinguishes them from other pachythecaliines. However, progressive trends of increased integration are observed in several groups of reef-building, modular invertebrates, including corals (e.g., Coates and Oliver, 1973; Coates and Jackson, 1985; Roniewicz and Stolarski, 1999; Wood, 1999). Some of the diagnostic characteristics for pachythecaliines might have been lost in some lineages (see Stolarski and Russo, 2001). A good example is bilateral symmetry of the septal apparatus. Such a septal pattern is characteristic for amphiastraeids. However, *Quenstedtiphyllia* Melnikova (subfamily Quenstedtiphylliinae) has quasi-ra-

dial symmetry in the adult stage (Ronie- wicz and Stolarski, 2001). Recently, Löser (2012) has distinguished a new, amphiastraeid genus *Hexamphiastrea*, similar to *Metaulastrea* (= *Amphiaulastrea*), but showing radial symmetry (see also *Amphiaulastrea suprema* in Morycowa and Marcopoulou-Diacantoni, 1997, 2002). Differences in morphology of the septa between the new genus and other amphiastraeids, as well as the lack of information about Taschenknospung budding, raise a question about the systematic position of *Hexamphiastrea*. Still, it is morphologically closest to amphiastraeids than to other corals.

Even assuming differences in the microstructure between different pachythecaliine groups, the possibility of phylogenetic relationships is not excluded (cf. Roniewicz and Stolarski, 2001, p. 36), because evolution of the skeleton microstructure of pachythecaliines also should be taken into account. Therefore, it seems reasonable to consider a combination of features, when phylogenetic relationships are studied. Molecular data on modern corals support the usefulness of skeleton microstructure and morphology in classifications at the family level, but on the other hand, found their grouping into suborders to be debatable (e.g., Romano and Palumbi, 1996; see also Stolarski and Roniewicz, 2001). It is particularly important, if we consider classifying pachythecaliines within a separate order (see below).

Position of Pachythecaliina within Anthozoa

The other debatable question is the position of pachythecaliines within the class Anthozoa and their possible relationship to Palaeozoic corals. These corals were usually, or still are, classified within the order Scleractinia. However, recognition of the unique, skeletal features of pachythecaliines led to their also being considered as rugosan corals (Koby, 1888; Ogilvie, 1897) or survivors of the Rugosa (Alloiteau, 1957; Cuif, 1975, 1977, 1981, 2010; Melnikova and Roniewicz 1976; Stolarski, 1996; Cuif and Stolarski, 1999). Montanaro Gallitelli (1975) distinguished the new order Hexanthiniaria, intermediate between the Rugosa (plerophyllines) and the order Scleractinia, and classified here a new Upper Triassic family Zardinophyllidae. Later Eliášová (1976b) included in the Hexanthiniaria in the suborder Pachythecaliina (with the family Pachythecalidae Cuif, 1975, a younger synonym of Zardinophyllidae), Amphiastraeina (Pachythecaliina *sensu* Roniewicz and Stolarski, 2001), Carolastraeina and Heterocoeniina. Recently, this systematic position of Pachythecaliina was accepted by Roniewicz (2008), Morycowa (2012) and Melnikova and Roniewicz (2012). It is also accepted in the present paper. However, the concept of Pachythecaliina should be re-examined with regard to its diagnostic features, both in terms of skeletal morphology, septal pattern and significance of the microstructure as diagnostic feature of the pachythecaliines The broad range of septal pattern in pachythecaliines, from (1) "rugosan"-like in *Zardinophyllum*, and (2) corallites with few or only one recognizable septum (*Pachythecophyllia*, *Monoaulastrea*; see Kołodziej, 2003; Löser *et al.*, 2009) to (3) scleractinian-like septal pattern as in the adult stage of *Carolastraea* and *Paracarolastraea* at the end of the spectrum is a challenge in establishing the diagnostic criteria for pachythecaliines. However, as discussed above, some "typical" pachythecaliine skeletal features could have been lost in some lineages.

Further research is needed, particularly in dealing with septal insertion. Montanaro Gallitelli (1974, 1975) and Stolarski (1996) observed in *Zardinophyllum* a rather broad, intraspecific variability in metaseptal insertion, however, without a typical rugosan, septal pattern. Interestingly, the drawings, presented by Lebanidze (1991), show septal insertion in amphiastraeid *Mitrodendron ogilviae* Geyer, 1955 similar to the one in the Rugosa, but it was never verified and documented in photographs. Stolarski (1996) hypothesized that some rugosans might have survived the P/T extinction in refuges and realized their potential, with modifications to their skeleton mineralogy and septal insertion. Thus some Permian, scleractiniamorphs might be the ancestors of some Triassic corals (see references above), whereas other scleractinian lineages might have evolved from soft-bodied (corallimorpharian-like) ancestors, as is commonly assumed (e.g., Stanley, 2003). The discovery of Late Cretaceous, solitary corals with an original calcitic skeleton indicates that some scleractinian corals indeed may secrete skeletons of different carbonate polymorphs (Stolarski *et al.*, 2007). The long lasting discussion on Triassic corals, representing the family Zardinophyllidae (= Pachythecaliidae), and their supposed relationship to some Late Palaeozoic corals is still not expressed in the commonly accepted, higher-rank classification. Recently, Cuif (2010) summarized some ideas on the possible relationships between some scleractinians and rugosans and called for a re-examination of the present concept of the Scleractinia. The hypothesis on the phylogenetic relationships between the skeletal Palaeozoic corals and corals from the suborder Pachythecaliina/Amphiastraeina (or in general Scleractinia) was challenged by researchers of rugosans and other Palaeozoic corals, including Permian scleractiniamorphs (Oliver, 1980a, b, 1996; Fedorowski, 1997; Scrutton, 1997; Ezaki, 2004).

Spatial and temporal proliferation of phaceloid pachythecaliines

The first pachythecaliines – the Zardinophyllidae and two genera from the Amphiastraeidae – are known from the Upper Triassic (Montanaro Gallitelli, 1974, 1975; Cuif, 1975; Roniewicz and Stolarski, 2001). Since the Late Jurassic, pachythecaliines became more common, but still were poorly diversified. Usually only some species occur in Oxfordian–Kimmeridgian coral assemblages (e.g., Roniewicz, 1966: two genera, two species; Roniewicz, 1976: five genera, seven species). However, they are highly diversified and abundant (and largely phaceloid) in the Tithonian–Lower Berriasian Štramberk Limestone in Czech Republic, Outer Carpathians (17 genera, 35 species; Ogilvie, 1897; Geyer, 1955; Eliášová, 1974, 1975, 1976a, b, 1978) and in pebbles/boulders (so called exotics) of the Štramberk-type limestones from Poland (14 genera, 22 species; Ogilvie, 1897; Geyer, 1955; Morycowa, 1964b, 1974; Kołodziej, 1995, 2003). Owing to the displaced character of these limestones (huge olistoliths in Štramberk, pebbles and boul-

ders in the Polish Carpathians), the precise age of particular coral specimens/taxa from these limestones cannot be specified. On the basis of calpionellids, a Tithonian–Early Berriasian age is commonly accepted for the coral-bearing limestones (Morycowa, 1968, 1988; Houša, 1990; Ciborowski and Kołodziej, 2001), but it is possible that reefs were developed mainly during the Late Tithonian. Locally sedimentation of Štramberk-type limestones in the Polish segment of northern part of Tethys (mostly in lagoonal facies) continued until the Valanginian (see Morycowa, 1988; Ivanova and Kołodziej, 2010). In most papers on corals from the Štramberk Limestone, the age was determined as Tithonian (see Vašíček and Skupien, 2004 for references). For the reasons mentioned above, corals from the Štramberk Limestone are usually recorded in the literature and databases as Jurassic, not Cretaceous fauna. However, for the discussion of evolutionary trends it is important that until the Valanginian, coral assemblages have a "Late Jurassic character" (Roniewicz and Morycowa, 1993), recently exemplified by a detailed study of corals from the continuous, Kimmeridgian–Valanginian succession in SW Bulgaria (Roniewicz, 2008).

During the Barremian and Aptian, a time span with the highest coral development in the Early Cretaceous (Löser, 1998), phaceloid pachythecaliines were rare. Only a widespread proliferation of heterocoeniids, mostly with a cerioid-plocoid type of colony, is observed in the Cretaceous (see citation lists in Löser *et al.*, 2002). The richest Early Cretaceous assemblage of pachythecaliines, except for heterocoeniids, was described by Baron-Szabo and Steuber (1996) from the Aptian of Greece. They recognized 10 genera and 13 species (including two heterocoeniid genera and two species), but only two genera and three species are phaceloid.

In summary, a prolific development of phaceloid pachythecaliines in the Tithonian and Berriasian, possibly mainly in the Late Tithonian (Czech Republic, Poland), in the Late Barremian (Bulgaria), and to a smaller extent in the Aptian (Greece), occurred in palaeogeographically restricted areas, with poorly known, environmental constraints.

SYSTEMATIC PALAEONTOLOGY

(by Bogusław Kołodziej)

Abbreviations: UJ 225 P – x 1 – x refers to the sampling site (Ru – Rusalya, Vis – Vishovgrad, Zar – Zarapovo, Hot – Hotnitsa) and the specimen number from the collection UJ 225 P (Institute of Geological Sciences, Jagiellonian University, Kraków); **UJ 225 P – x/1** – numbers 1, 2, 3 *etc.* refer to the thin section number from a given sample; **ZPAL – Bulg 1/1** – number of the sample (Bulg 1/x) and thin section (Bulg 1/1), housed at the Institute of Palaeobiology, Polish Academy of Sciences, Warszawa.

Measurements used in descriptions are abbreviated as follows: **d** – corallite diameter (in mm); **c–c** – distance between corallite axes (in mm); **s** – number of septa; **S1... Sn** – septa of succeeding size orders; **number of the sample in bold** – samples presented on figures; **( )** – less frequent values are given in brackets.

Order HEXANTHINIARIA Montanaro-Gallitelli, 1975
Suborder PACHYTHECALIINA Eliášová, 1976
Family AMPHIASTRAEIDAE Ogilvie, 1897
Subfamily AMPHIASTRAEINAE Ogilvie, 1897

Remarks: Roniewicz and Stolarski (2001) established the new subfamily Quenstedtiphylliinae containing the genus *Quenstedtiphyllia* Melnikova, 1975 from the Upper Triassic. This subfamily differs from the subfamily Amphiastraeinae by one-zonal (tabular) endotheca and corallites with quasi-radial symmetry in the adult stage. In the case of poorly preserved specimens, skeletal structures in longitudinal section (e.g., type of endotheca) are difficult to decipher. Recently, Löser (2012) established the genus *Hexamphiastrea* with the type species *Amphiaulastrea suprema* Morycowa et Marcopoulou-Diacantoni (Morycowa and Marcopoulou-Diacantoni, 1997, 2002). *Hexamphiastrea* is close to *Metaulastrea* Dietrich and *Amphiastrea* Étallon but has hexameral symmetry and thick rhopaloid septa. However, owing to the septal morphology of *Hexamphiastrea*, its classification in the Amphiastraeidae is under question.

Genus *Metaulastrea* Dietrich, 1926
Type species: *Aulastrea pompeckji* Dietrich, 1926

Remarks: Löser (2008c) replaced *Amphiaulastrea* Geyer, 1955 with *Metaulastrea*. *Metaulastrea* was provisionally established by Dietrich (1926), but it is valid, according to the International Code of Zoological Nomenclature (Ride *et al.*, 1999; see Löser, 2008c). According to Löser (2008c), the type specimen of the type species (*Aulastraea conferta* Ogilvie, 1897), selected by Geyer (1955), does not represent *Amphiaulastrea*. From the Cretaceous, seven species of *Metaulastrea* (=*Amphiaulastrea*) are known (see citation lists in Löser *et al.*, 2002). Thus, apart from *Amphiastrea* (about ten species), it is the most diversified genus among the Cretaceous amphiastraeids.

Metaulastrea cf. *rarauensis* (Morycowa, 1971)
Fig. 10

Material: Six samples, six thin sections.
Measurements: Morphometric measurements are presented in Table 1.

Table 1

Dimensions (in mm) of *Metaulastrea* cf. *rarauensis* (Morycowa, 1971)

Sample number UJ 225 P -	d	c–c	s
Vis 5	4-5 × 7–10	6–9	up to 45
Vis 10	6-7 × 7–11	(5) 6–8 (9)	up to 50
Vis 26	6-9 × 9–12	7–10	?
Vis 44	4-6 × 6–9	5–7	up to 43
Ru 3-10	4-5 × 5–7	5–6	up to 40
Ru 14	5–11	5–7	up to 35

Remarks: The samples studied are determined in open nomenclature as *Metaulastrea* cf. *rarauensis* (Morycowa). *M. rarauensis*, described from Lower Aptian of Romania (Morycowa, 1971), was also recognized from the Valanginian to Aptian of Greece, Ukraine, Turkmenistan and Azerbaidjan, but mostly was not illustrated (see Löser *et al.*, 2002). New species, established by Baron-Szabo (Baron-Szabo and Steuber, 1996) as *Amphiaulastraea keuppi*, is considered as a younger synonym of *M. rarauensis*. This species is also known from Barremian–Lower Aptian marls of the Lovech

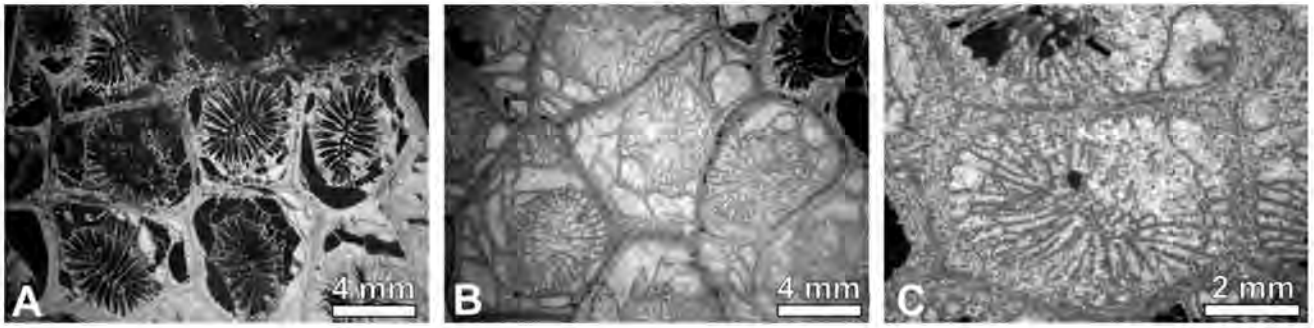


Fig. 10 *Metaulastrea* cf. *rarauensis* (Morycowa). **A, B** – corallites with well developed marginarium. **C** – corallite with poorly developed marginarium. UJ 225 P; A – Vis 10/1, B – Vis 26/1, C – Vis 44/1

Urgonian Group (Idakieva, 2003). The peripheral part of the calicular space (containing shorthest septa) in the samples studied is commonly filled with calcite spar cement and the septa are recrystallized. As a result, the exact counting of septa is difficult. Differences in measurements revealed in the specimens seem to reflect intraspecific variability, rather than the presence of more species. However, more thin sections are required to obtain detailed measurements.

Distribution: Lower part of middle Upper Barremian (Rusalya, Vishovgrad).

Genus *Amphiastrea* Etallon, 1859
Type species: *Amphiastrea basaltiformis* Etallon, 1859

Amphiastrea sp.
Fig. 11

Material: One sample (UJ 225 P – Ru 9-08), one thin section.
Measurements (in mm): d = 6–7 (8), c–c = 5–7, s = up to 23.
Remarks: Locally, the minute interstices between adjacent corallites are filled with sediment. These interstices may be due to a poor state of preservation or may reflect subcerioid (with closely packed *basaltiformes* corallites). *Amphiastrea*, usually described as a cerioid coral, displays in fact a pseudocerioid growth form, with each corallite having its own wall (Morycowa and Lefeld, 1966; Melnikova and Roniewicz, 1976; Roniewicz and Stolarski, 1999, 2001). Such a growth form can be recognized, only if the lateral surfaces of corallites can be observed as covered by epitheca (see Ogilvie, 1897; Geyer, 1955; Morycowa, 1964b).
Distribution: Lower part of middle Upper Barremian (Rusalya).

Genus *Pleurophyllia* de Fromentel, 1856
Type species: *Pleurophyllia trichotoma* de Fromentel, 1856

Remarks: *Pleurophyllia* is rarely reported from the Cretaceous, whereas in the Late Jurassic it was a relatively common genus among amphiastraeids. Löser *et al.* (2002) cited only a few records of this genus in the Cretaceous and only two species, *P. trichotoma* de Fromentel and *P. skuviensis* Turnšek. According to Roniewicz (2008), *P. skuviensis* described by Turnšek (in Turnšek and Mihajlović, 1981) from the Barremian–Lower Aptian of Serbia represents the genus *Cladophyllia* Milne Edwards et Haime, 1851. *P. trichotoma*, described by Sikhuralidze (1979) from Georgia, is possibly from the Upper Jurassic, not the Albian. Other Lower Cretaceous specimens are determined in open nomenclature, but they are too poorly documented to confirm their taxonomic determinations. In the limestones studied, *Pleurophyllia bulgarica* sp. nov. is the most common coral.

Although a phaceloid corallum is characteristic for this genus, a densely packed to subcerioid growth form may occur locally in the specimens studied. This is in accordance with the recent redescription of the syntype of the type species *Pleurophyllia trichotoma* by Lathuilière (2012a): "Probably phaceloid corallum (the polished syntype shows on one side a single corallite and on the other face, in correspondence, a set of three corallites not yet separated)". It is worth emphasizing that a mixed growth form of corallum occurs in some other pachythecaliine taxa. A dendroid-phaceloid to subcerioid growth form occurs in amphiastraeids *Aulastrea* Ogilvie, 1897, *Hykeliphyllum* Eliášová, 1975 (e.g., Geyer, 1955; Eliášová, 1975), and in *Pleuroaulastrea variabilis* gen. et sp. nov, described below, and in particular in ?*Pleurophyllia* sp. These examples give evidence of the high potential of some pachythecaliines for variability of growth form, which might be favoured by low, biological integration in these corals. According to Coates and Oliver (1973), who discussed rugosan corals, cerioid corallum is only a compact, phaceloid corallum. Many Recent and fossil corals show a response of growth forms to environmental factors (e.g., Young, 1999a and literature therein). However, mixed, cerioid-phaceloid growth forms are not common in scleractinian corals (Lathuilière, 1989, 1996). A changing growth pattern may have no systematic significance, but may be interpreted as a partial death of the colony, due to sedimentation or predation (Lathuilière, 1989), or reflects only close packing, which resulted from space compaction. Mixed growth forms of corals occur more commonly in the Rugosa. Partly phaceloid/partly cerioid coralla occur in rugosan Lithostrotionidae (e.g., Nudds, 1979) and Phillipsastreidae (e.g., Wrzołek, 2007). Some rugosan corals show changes in colony type – from cerioid to fasciculate (branching) – during regeneration (Fedorowski, 1980; Poty, 1981; Young, 1999b).

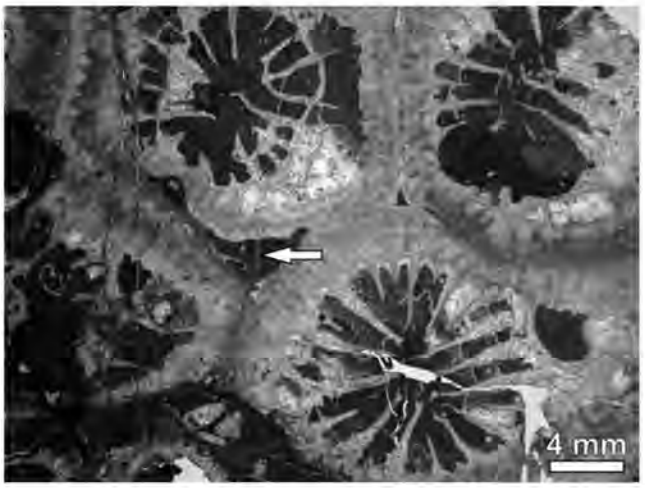


Fig. 11. *Amphiastrea* sp. Arrow indicates inter-corallite interstice filled with sediment. UJ 225 P – Ru 9-08/1

Pleurophyllia bulgarica new species, Kołodziej
Fig. 12

Holotype: UJ 225 P – Ru 14-08.
Paratypes: UJ 225 P – Ru 19-08, Ru, 21, Ru 30, Ru 7257, Ru 8837, Ru 8860.
Etymology: *bulgarica* – from the country name Bulgaria.
Type locality: Rusalya, Bulgaria.
Type level: Lower part of middle Upper Barremian, Emen Formation, Bulgaria.
Stratigraphic distribution: Lower part of middle Upper Barremian.
Diagnosis: *Pleurophyllia* of corallite diameters ranging from (4) 5 to 9 (12) mm and number of septa up to 49.
Material: 17 samples, 30 thin sectionsn (13 large), one polished slab.
Measurements: Morphometric measurements are presented in Table 2.

Table 2

Dimensions (in mm) of *Pleurophyllia bulgarica* sp. nov.

Sample number UJ 225 P -	d	s
Holotype Ru 14-08	(5) 6–7 × 6–8 (11)	up to 32
Paratype Ru 19-08	(4) 5–8 × 7–9 (10)	up to 38
Paratype Ru 21	(4) 5–7 × 6–9	up to 32
Paratype Ru 30	4–6 × 4–8 (9)	up to 39
Paratype Ru 7257	(4) 5–6 (7) × 6–9 (12)	up 49
Paratype Ru 8837	(4) 5–7 × 7–9	up 41
Paratype Ru 8860	4–7 × 6–8 (9)	up to 38
Ru 1-10	4–8	?
Ru 2	(4) 5–7 × (6) 7–10	up 34
Ru 4-08	5–6, longest up to 10	up 32
Ru 7-08	4–6 × 5–10	up to 32
Ru 13-08	5–9 × (5) 8–12	up to 41
Ru 15-08	5–8 × 6–10	up to 40
Ru 17-08	4–8 × 6–10	up to 32
Ru 249	5–10	up to 35
Vis 1673	6–11	up to 34
Hot 1	6–10	up to 35

Description: Phaceloid corallum. Locally, corallites are close to each other, resulting in a subcerioid growth form. Corallites in transverse section are more or less elongated, rarely round. Septa arranged in bilateral symmetry, defined by longer septa on one side of corallite, but with the primary septum usually only slightly longer and thicker than others. Septa smooth and thin, although thick septa may occur in some corallites. Lonsdaleoid septa present. Endotheca two-zonal, built by large tabuloid dissepiments in the central part and vesicular dissepiments in the narrow peripheral zone. Marginarium in corallites rarely observed. Discontinuous "exfoliation" of wall recognized in one corallite. Taschenknospung budding.

Remarks: As in many other species, described in the present paper, differences in the number of septa depend partly on the state of preservation. At the peripheral part of corallites, septa are difficult to count also, because they are poorly and irregularly developed there (possibly also as septal spines like in heterocoeniids; cf. Morycowa, 1971; Kołodziej, 1995). *Pleurophyllia bulgarica* sp. nov. differs from *P. trichotoma* (known from the Upper Jurassic and Berriasian) in larger corallite diameters and more abundant septa. For example, *P. trichotoma*, described by Roniewicz (1966): d 6–8, s 20 (24); Eliášová (1975): d 5–7 (8.5), s 20 + S3; Kołodziej (2003): d (5) 6–8, s 20–30. Other known species of *Pleurophyllia* have smaller diameters and smaller numbers of septa. *P. trichotoma* shows bilateral symmetry, defined by a well developed, primary septum, which in the new species is poorly developed, although bilateral symmetry is well marked. On the other hand, a "main sector", as in *Hykeliphyllum* Eliášová and *Psudopistophyllum* Geyer does not occur. A skeletal structure, resulting from "exfoliation" (poorly preserved marginarium?) of a wall, similar to the one observed in *Paracarolastraea zlatarskii* gen. et sp. nov., was recognized only in one corallite (Fig. 12K). The greatest differences are in the specimen from Hotnitsa, where the "main sector" is more clearly developed (Fig. 12F, G).
Distribution: Lower and middle parts of Upper Barremian (Hotnitsa, Rusalya, Vishovgrad).

?*Pleurophyllia* sp.
Fig. 13

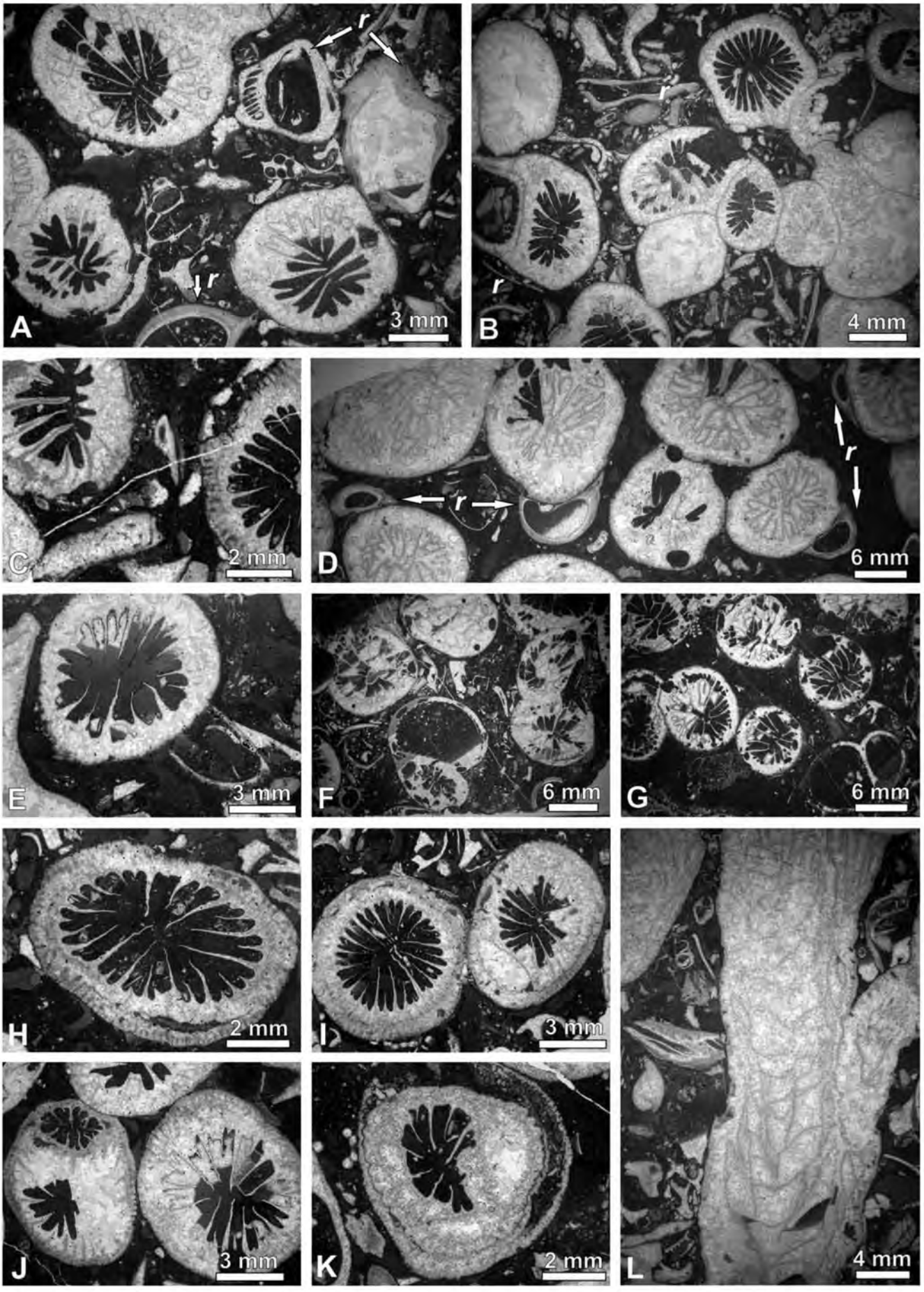
Material: One sample (UJ 225 P – Ru 7262), one large thin section.
Measurements (in mm): d = (4) 5–7 (8), s = up to 31.
Remarks: The coral shows mixed phaceloid (*Pleurophyllia*-like) to subcerioid (*Amphiastrea*-like) growth forms. The small piece of the sample does not permit determination of whether it is a fragment of a pseudocerioid-dominated or phaceloid-dominated corallum. Corallites are particularly poorly preserved in the phaceloid part. The interskeletal space is filled here with sparite cement, thus analysis of the septal apparatus is not possible, but the marginarium can be recognized in some corallites. The relation between corallites of the subcerioid and phaceloid parts of the corallum excludes the possibility of fusion of two different corals. As described above, the subcerioid growth form may locally occur in *Pleurophyllia bulgarica* sp. nov. and in the type species of *Pleurophyllia*.
Distribution: Lower part of middle Upper Barremian (Rusalya).

Genus *Aulastrea* Ogilvie, 1897
Type species: *Aulastrea schäferi* Ogilvie, 1897

?*Aulastrea touli* new species, Kołodziej
Fig. 14

Holotype: UJ 225 P – Vis 2.
Etymology: *touli* – in honour of Franz Toula, 19th Austrian coral researcher of Cretaceous corals in Bulgaria.
Type locality: Vishovgrad, Bulgaria.
Type level: Lower part of middle Upper Barremian, Emen Formation, Bulgaria.

Fig. 12. *Pleurophyllia bulgarica* sp. nov. **A–K** – transverse sections, **L** – longitudinal section. **A, B, D** – *r* indicates small rudists, mostly *Mathesia darderi* (Astre), particularly numerous in D. B – densely packed corallites. **C** – two corallites with septa of variable thickness. **F, G** – corallites with quasi main sector. **H, K** – corallites with 'exfoliation' of wall (compare Fig. 17). **J** – corallites with Taschenknospung budding. UJ 225 P; A – Ru 14-08/2, B – Ru 8860/1, C – Ru 8837/1, D – Ru 7257/3, E, I – Ru 30/1, F, G – Hot 1/2, H, J – Ru 19-08/2, K – Ru 4-08/1, L – Ru 249/1. A – holotype, B, C, E, H, I, J – paratypes


A
r
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3 mm
B
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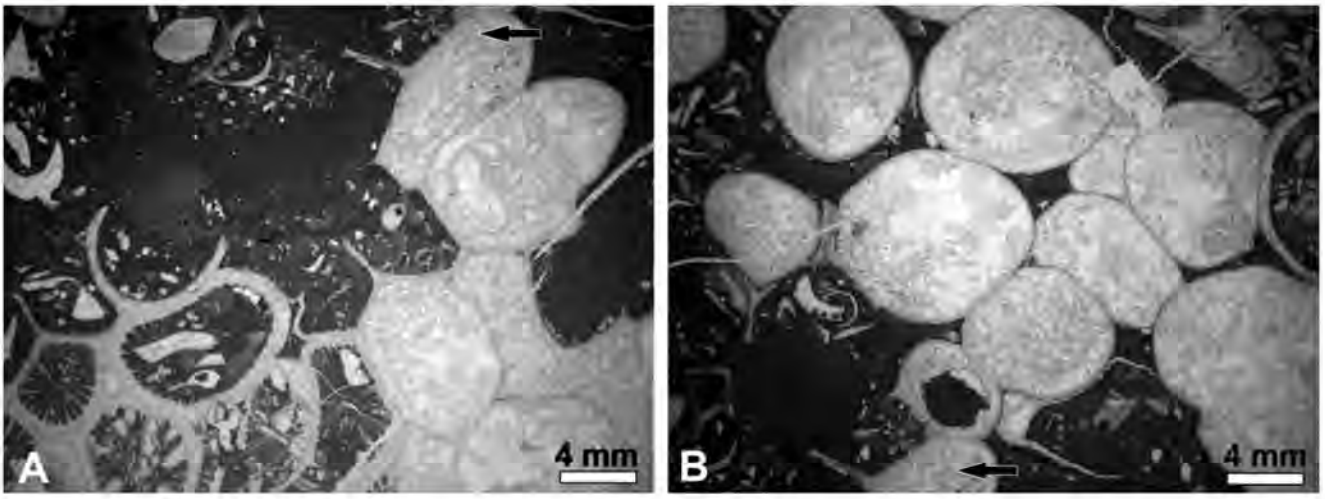

Fig. 13. ?*Pleurophyllia* sp., displaying, mixed subcerioid (**A**) to phaceloid growth form (**B**). Arrows indicate corallite, linking subcerioid and phaceloid parts of corallum. UJ 225 P – Ru 7262/1

Stratigraphic distribution: Lower part of middle Upper Barremian.

Diagnosis: Dominantly phaceloid, locally phaceloid-dendroid to subcerioid corallum. Corallites from about 7 mm to 21 mm in diameters, and up to 50 septa.

Material: One sample (UJ 225 P – Vis 2), four large thin sections, three polished slabs.

Measurements (in mm): d = 7–21, s = highly variable, up to at least 50.

Description: Phaceloid, locally a phaceloid-dendroid to subcerioid corallum. Locally corallites form compact clusters. Corallites oval. Septa arranged in bilateral symmetry. Septa on one side of corallite are longer, but a primary septum is only slightly longer and slightly thicker. Lonsdaleoid septa present. Complete marginarium developed around the septal apparatus only in some corallites; in others, marginarium is poorly developed ("marginal pockets"). Endotheca in peripheral zone built of vesicular dissepiments; in central part poorly preserved, but possibly built of tabuloid dissepiments. Taschenknospung budding.

Remarks: The new species is tentatively assigned to the genus *Aulastrea*. It differs from *Aulastrea* in its growth form. *Aulastrea* has a massive subcerioid to dendroid-phaceloid corallum, with short branches and a conical lower part (see Ogilvie, 1897; Geyer, 1955; Eliášová, 1975; Schäfer and Senowbari-Daryan, 1980; Lathuilière, 2012b). In contrast to *Aulastrea*, there is a lack of a distinct, thick, primary septum. The septal pattern is similar to the one, occurring in *Pleurophyllia bulgarica* sp. nov. *Aulastrea* is poorly known from the Lower Cretaceous (see citation lists in Löser *et al.*, 2002). The best documented in the Cretaceous are *Aulastrea schaeferi* Ogilvie, 1897 and *Aulastrea* cf. *macer* Eliášová, 1975 described by Baron-Szabo (in Baron-Szabo and Steuber, 1996) from the Aptian of Greece, previously known only from the Upper Jurassic/earliest Cretaceous.

Distribution: Lower part of middle Upper Barremian (Vishovgrad).

Genus *Pleuroaulastrea* new genus, Kołodziej
Type species: *Pleuroaulastrea variabilis* sp. nov., Kołodziej

Etymology: In relation to *Pleurophyllia* and *Aulastrea*.

Diagnosis: Corallum phaceloid, locally subcerioid. Corallites round or slightly oval, and highly variable in diameter. Septa arranged in bilateral symmetry, defined by long axial primary septum. Lateral septal faces covered by small granules. Marginarium present. Lonsdaleoid septa present. Endotheca unknown. Taschenknospung and parricidal budding.

Stratigraphic distribution: Lower part of middle Upper Barremian.

Remarks: *Pleuroaulastrea* gen. nov. differs from *Aulastrea* in the general corallum growth form (see remarks on ?*Aulastrea touli* sp. nov.). In the new genus, the marigarium is poorly developed and not complete. Corallites are highly variable in size. The septal pattern in small corallites is close to *Pleurophyllia*. Apart from Taschenknospung, parricidal budding occurs, resulting in a partial, subcerioid growth form, built of small polygonal corallites. Figure 16A, B shows recrystallized corallites with parricidal budding. This budding type is similar to the one, occurring in *Mitrodendron* Quenstedt, 1880 (Roniewicz, 1966, text-fig. 15; pl. 16, fig. 1c; Melnikova and Roniewicz, 1976, fig. 4; Roniewicz, 2008, fig. 3c), in which new budds appear on the endothecal elements. It differs from the parricidal budding in *Intersmilia* Eliášová, 1974, where septa of a parent individual continue into a daughter one (Melnikova and Roniewicz, 1976, fig. 4; see also remarks on *Intersmilia* aff. *diaboli* Eliášová, 1974 in the present paper).

Pleuroaulastrea variabilis new species, Kołodziej
Figs 15, 16

Holotype: UJ 225 P – Vis 1.

Etymology: *variabilis* – for its high variability in corallite diameter and corallum growth form.

Type locality: Vishovgrad, Bulgaria.

Type level: Lower part of middle Upper Barremian, Emen Formation, Bulgaria.

Stratigraphic distribution: Lower part of middle Upper Barremian.

Diagnosis: *Pleuroaulastrea* with highly variable corallite size, from 4–8 mm in the subcerioid/densely phaceloid part of the corallum to 10–27 mm in the phaceloid part. Number of septa relatively small, up to 29.

Material: One sample (UJ 225 P – Vis 1), seven thin sections (two large), eight polished slabs.

Measurements (in mm): d = 4–8 in subcerioid/densely phaceloid part of corallum 10–27 in phaceloid part of corallum, s = up to 29 (in large corallites).

Description: Phaceloid corallum. Locally corallites, resulting from parricidal budding, are close to each other, resulting in sub-

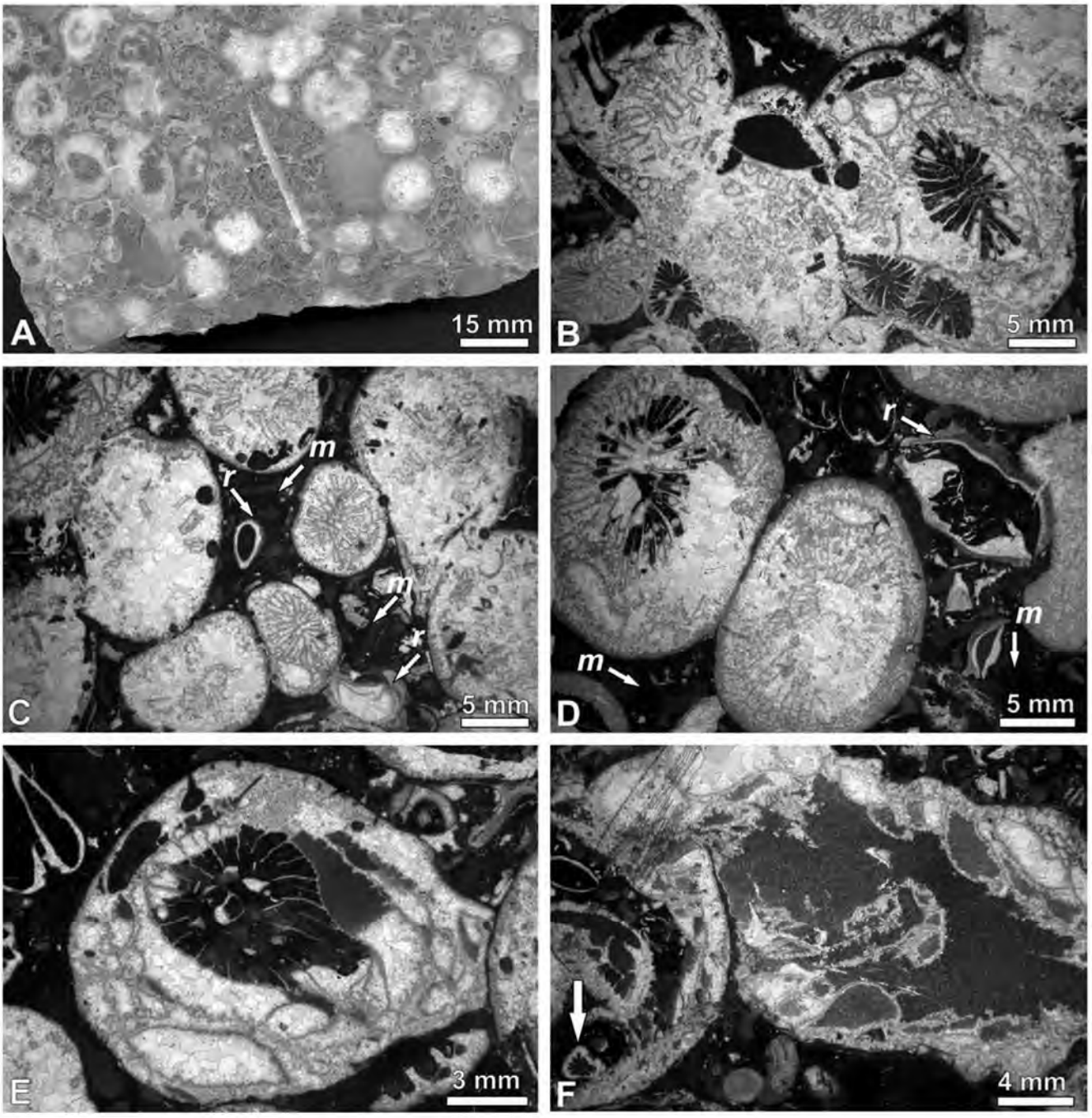

Fig. 14. ?*Aulastrea touli* sp. nov., holotype UJ 225 P – Vis 2. **A** – polished slab of holotype specimen. Corallites strongly recrystallized; interskeletal space commonly filled with calcite spar cement, in particular in peripheral parts of corallites. **B** – dendro-phaceloid to subcerioid part of corallum with Taschenknospung budding (Vis 2/2). **C, D** – corallites with poorly developed marginarium; arrows indicate small rudists (*r*) and small microbialite 'bridges' (*m*) between coral branches (C – Vis 2/2, D – Vis 2/1). **E** – corallite with broad marginarium (Vis 2/2). **F** – longitudinal section showing large, vesicular dissepiments at the peripheral part of endotheca. At left side, transverse to slightly oblique section displays small parricidal bud (arrow) (Vis 2/4)

cerioid growth form. Corallites round or slightly oval. Diameter of corallites is highly variable in diameter; they are significantly smaller in the subcerioid part of corallum. Septa arranged in bilateral symmetry, defined by long, axial, primary septum. Lateral faces of larger septa are covered by small granules. Marginarium well or poorly developed. Lonsdaleoid septa present. Endotheca unknown. Taschenknospung and parricidal budding.

Distribution: Lower part of middle Upper Barremian (Vishovgrad).

Family CAROLASTRAEIDAE Eliášová, 1976

Remarks: Until now Carolastraeidae contained only one genus *Carolastraea* Eliášová, 1976 with three species. Löser (2009) included this genus in the Amphiastraeidae.

Genus *Paracarolastraea* new genus, Kołodziej

Type species: *Paracarolastraea zlatarskii* sp. nov., Kołodziej

Etymology: *Paracarolastraea* – for similarity to *Carolastraea* Eliášová, 1976.

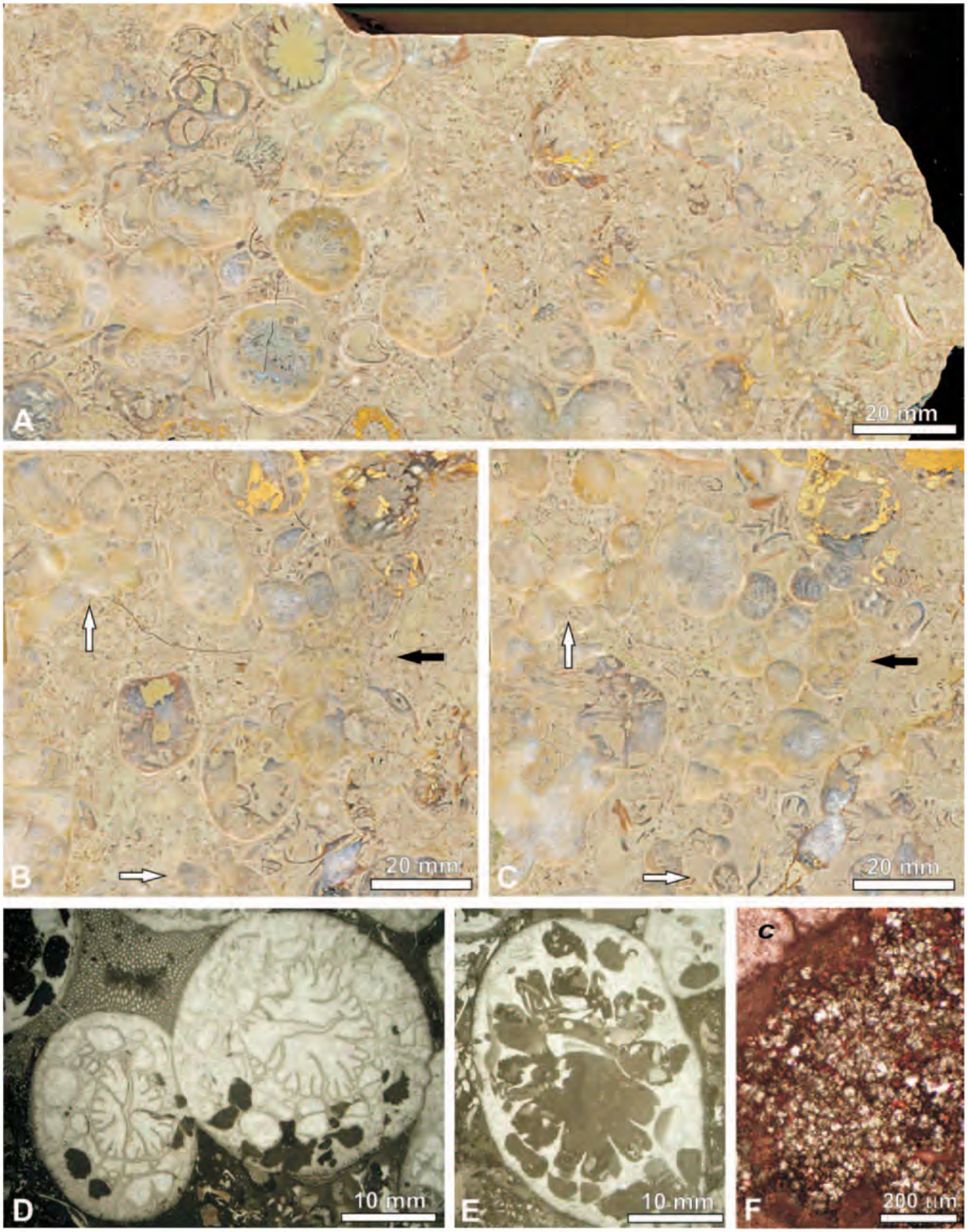

Fig. 15. *Pleuroaulastrea variabilis* gen. et sp. nov, holotype UJ 225 P – Vis 1. **A–C** – polished slabs of holotype specimen, showing high variability in corallite arrangement and size. **B** – polished slab, showing (black arrow) local, densely, packed polygonal corallites (subcerioid growth form). White arrows show densely packed rounded corallites. **C** – transverse section, made five millimeters above the surface on Figure B, with densely packed rounded corallites (black arrow). White arrows show loosely packed branches (compare with B). **D** – two corallites with well developed marginarium and bilateral symmetry, defined by long primary septum (Vis 1/2). **E** – corallite with destroyed, inner parts of septa (Vis 1/1). **F** – dolomite crystals in microbial automicrite (see Fig. 9B) in sample UJ 225 P – Vis 2/2. After staining of the thin section with Alizarine Red-S, only coral skeleton (*c*) and automicrite show reddish color

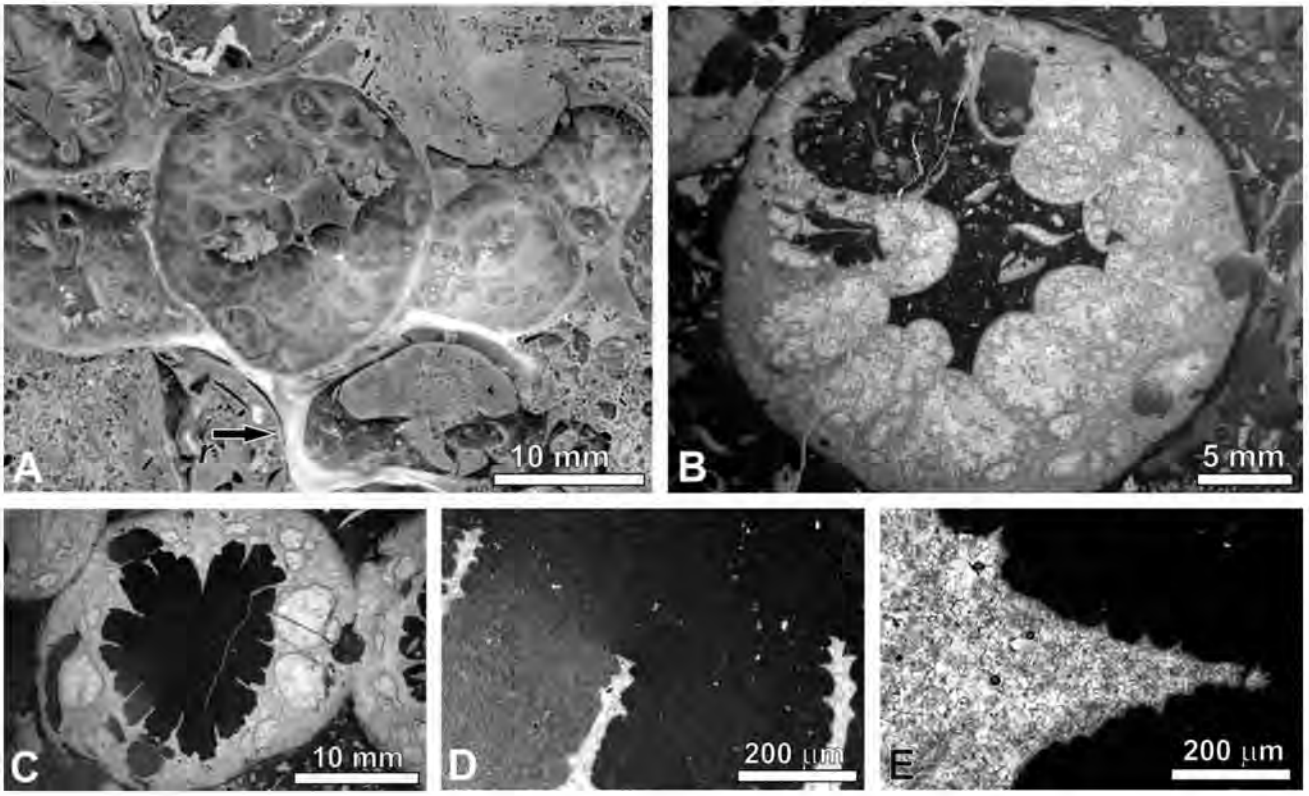

Fig. 16. *Pleuroaulastrea variabilis* gen. et sp. nov; holotype UJ 225 P – Vis 1. **A, B** – corallites with parricidal budding. Arrows in A show rudist shell (*r*). **C–E** – corallite with short septa possibly due to state of preservation; in D and E (enlargement of C), septa show granular ornamentation. **B–E** – thin section Vis 1/4

Diagnosis: Phaceloid corallum. Septa arranged in six subequal systems, in radio-bilateral symmetry. Larger septa are rhopaloid. A slightly enlarged, primary septum is present in some corallites. The wall is thick. Around the outer wall surface of some adult corallites there occur structures, resulting from a wall "exfoliation". These consist of one or more "layers", more or less parallel to the wall, and usually do not continuously surround it. Endotheca poorly preserved (one-zonal?). Budding extracalicular marginal and by septal division.

Stratigraphic distribution: Lower part of middle Upper Barremian.

Remarks: The new genus is similar to *Carolastraea* (Eliášová, 1976a). It differs in the presence of septal division and structures, resulting from a wall "exfoliation" (Fig. 17A–J) and in showing some analogy with marginarium in amphiastraeids. However, in contrast to the interseptal space in many corallites, the space between the wall and these structures is filled by sediment, not by sparite cement, implying that there were no dissepiments, which might close the space. In this respect, it differs from marginarium, which commonly contains dissepiments or septa (compare *Metaulastrea* cf. *rarauensis*, Fig. 10). Melnikova and Roniewicz (1976, p. 98) discussing the wall structure in *Mitrodendron ogilviae* Geyer and *Pleurophyllia trichotoma* de Fromentel from the Kimmeridgian of Poland, stated: "The wall develops in result of successive actions of skeletal secretion (pl. XXVIII, figs 1, 2), it is 'multilamellar' as was assumed by Beauvais (1974)". Melnikova and Roniewicz (1976, pl. 23, fig. 1) showed (vertical section) structures termed as "rudiments of calicular border" similar to those described in the preset paper and named here as structures resulted from wall "exfoliation".

Paracarolastraea zlatarskii new species, Kołodziej
Figs 17, 18 A–D

Holotype: UJ 225 P – Ru 34.

Paratypes: UJ 225 P – Ru 20-08, Ru 32, Ru 33.

Etymology: Named in honour of Dr. Vassil Zlatarski, a researcher of fossil and recent corals.

Type locality: Rusalya, Bulgaria.

Type level: Lower part of middle Upper Barremian, Emen Formation, Bulgaria.

Stratigraphic distribution: Lower and middle parts of Upper Barremian.

Material: Six samples UJ 225 P – Ru 20/08, Ru 31, Ru 32, Ru 33, Ru 34, Hot 1171; 16 thin sections (two large).

Diagnosis: *Paracarolastraea* with corallite diameter of 3–5 (6) mm, and 24 septa arranged in three size orders; very rare septa of the fourth order.

Description: Phaceloid corallum, only in places corallites are closely packed. In all samples corallite diameter is similar, ranging from 3 to 5 (6) mm. Septa arranged in six subequal systems, in radio-bilateral symmetry. Usually four of six S1 are longer and thicker than others. Larger septa (S1 and some S2) are commonly thickened at the inner margin (rhopaloid septa). A slightly enlarged primary septum occurs in some corallites (Fig. 17B, J). Septa S2 are S3 usually well developed, septa S4 rare. Septal faces are smooth or show faint, irregular granulations. Many adult corallites (up to 30% per thin section) contain structures resulting from "exfoliation" of the outer wall These structures usually discontinuously surround the wall. Endotheca poorly preserved (uni-zonal?). Budding extracalicular marginal and by septal division. Septal budding results in formation of two (Fig. 18A) or more daughter corallites (Fig. 18B–D).

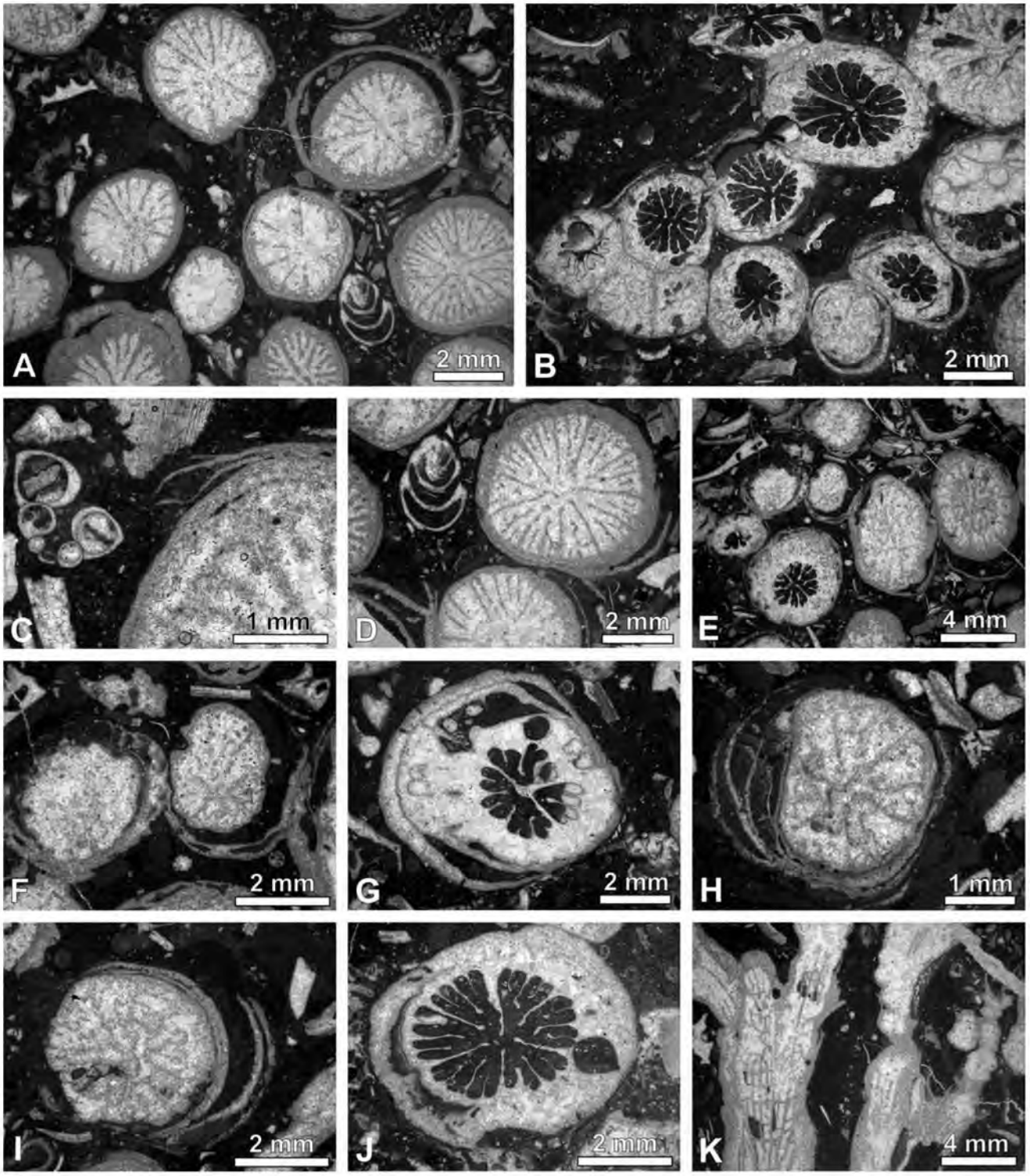

Fig. 17. *Paracarolastraea zlatarskii* gen. et sp. nov. **A–J** – transverse section. **K** – longitudinal section. Most of corallites on A–J show singular (A, B, J) or multiple (C–I) wall structures, resulting from 'exfoliation' of corallite wall. In G and H, these structures continuously surround corallite resulting in formation of some kind inner corallite. In B, corallites are highly variable in size and densely packed locally. UJ 225 P; A, C, D – Ru 34/4, B – Ru 34/3, E, F – Ru 34/4a, G – Ru 34/7, H, I, K – Ru 34/2. A–G, J – holotype, H, I– paratype

Remarks: With respect to diameter of corallites and number of septa the new species is similar to *Carolastraea gracea* Baron-Szabo, 1996 [corallites diameter (2.5) 3–4; number of septa (20) 24] from the Aptian of Greece (Baron-Szabo and Steuber, 1996). However, other features ('exfoliation' of a wall, septal increase) justify classification of the new species in the new genus *Paracarolastraea*. The septal division shows similarity to the one, reported in some Upper Triassic scleractinian corals (Roniewicz, 1989), and in the middle Permian scleractiniamorph, *Numidiaphyllum* (Ezaki, 2004), where both bipartite, as well as hexapartite and tripartite increases occur.

Distribution: Lower and middle parts of Upper Barremian (Rusalya, Hotnitsa).

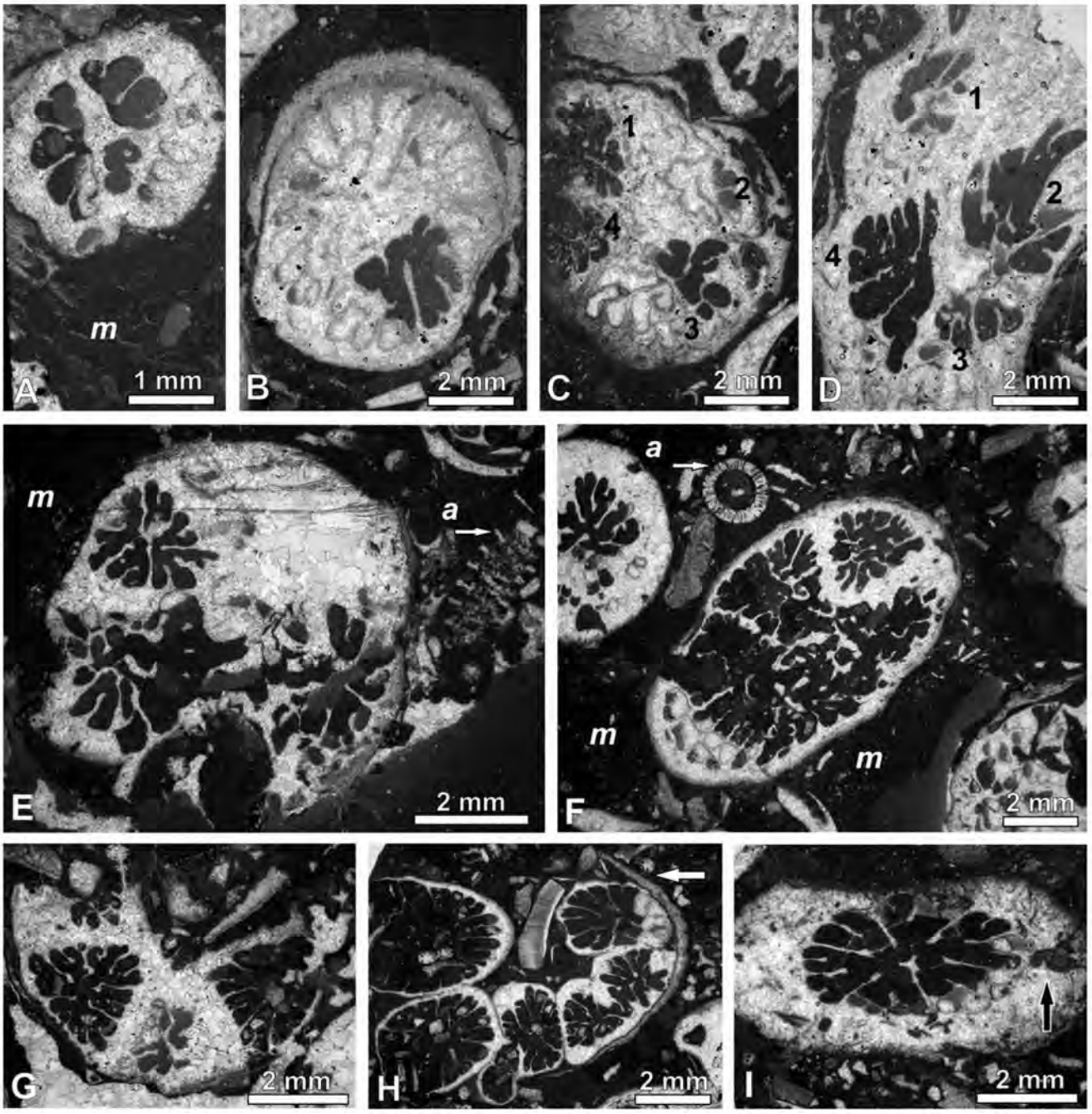

Fig. 18. **A–D.** Septal increase in *Paracarolastraea zlatarskii* gen. et sp. nov. In C and D, septal increase resulted in origin of four daughter corallites (numbered from 1 to 4); *m* in A indicates poorly laminated, microbialite crust. UJ 225 P; A – Hot 1171/1, B, D – Ru 32/1, C – Ru 32/2. **E–I.** ?*Paracarolastraea* sp. **E–H** – septal increase resulted in origin of a few daughter corallites. In H densely packed corallites are surrounded locally by common wall (arrow). *a* and *m* in E and F show dasyclad algae (E – *Zittelina hispanica* Masse, Arias et Vilas, F – *Neomeris* cf. *cretacea* Steinmann) and microbialite crust respectively. **I** – corallite with thick wall. Arrow possibly indicates early stage of blastogeny. UJ 225 P; E, G –Vis 40/1, F– Vis 30/1, I – Vis 30/2

?*Paracarolastraea* sp.
Figs 6A, 18E–G

Material: Two samples (UJ 225 P – Vis 30, Vis 40), three thin sections.

Remarks: Two specimens show similarities to *Paracarolastraea zlatarskii* sp. nov., with respect to diameter and number of septa, but they lack structures resulting from 'exfoliation' of the wall. Moreover, septal budding, resulting in the formation of even five daughter corallites (Fig. 18E–H), is more common, although only three thin sections were studied. In one thin section, a unique aggregation of corallites occurs. Densely packed corallites are surrounded locally by a common wall (possibly the wall of the parent individual). More serial sections are needed to reveal the exact increase pattern in this specimen, as well as its taxonomy (*Paracarolastraea zlatarskii* or a new species).

Distribution: Lower part of middle Upper Barremian (Vishovgrad).

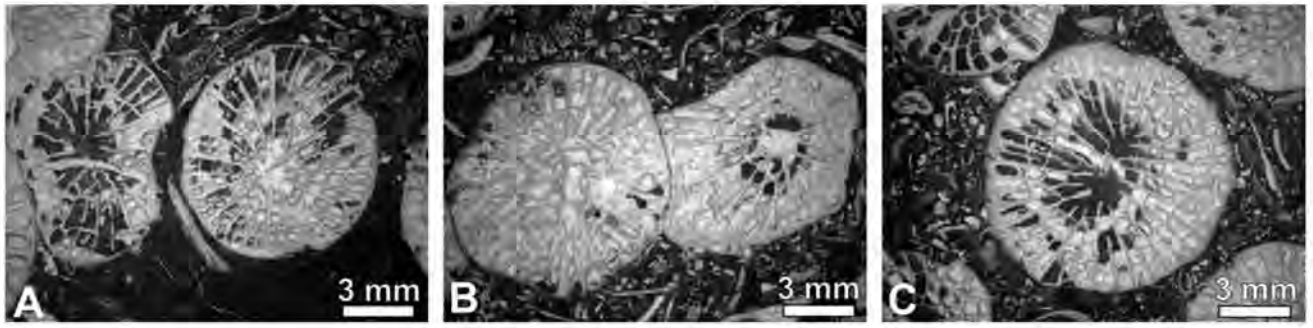

Fig. 19. ?*Donacosmilia* sp. **A–C** – transverse sections of corallites; note lack of marginarium and slightly bilateral symmetry. UJ 225 P – Ru 7270/1

Fig. 20. *Intersmilia* aff. *diaboli*. **A–C** – transverse sections of corallites; note dark color of wall. **C** – parricidal budding (arrow). ZPAL Bulg 3; A – 3/6, B – 3/4, C – 3/2

Family DONACOSMILIIDAE Krasnov, 1970
Genus *Donacosmilia* de Fromentel, 1861
Type species: *Donacosmilia corallina* de Fromentel, 1861

?*Donacosmilia* sp.
Fig. 19

Material: One sample (UJ 225 P – Ru 7270), one large thin section.
Measurements (in mm): d = (7) 8–10 (11), s = 41–47 (60) in adult corallites.
Remarks: Phaceloid corallum with some corallites, showing slightly marked, bilateral symmetry. Rare, lonsdaleoid septa present. The specimen described differs from the best known, Late Jurassic species *Donacosmilia corallina* de Fromentel and *D. etalloni* (Koby, 1888) (e.g., Turnšek, 1972, 1997; Melnikova and Roniewicz, 1976; Buzcu and Babayiğit, 1998) in having smaller corallite diameters and a greater number of septa. *D. massaliensis* Morycowa et Masse, 1998, from the Upper Barremian of Provence in France, shows smaller corallite diameters (6–7.5 mm) and less numerous septa (32 S1–S3 plus S4) (Morycowa and Masse, 1998). In the available fragment of corallum (15 corallites), no marginarium was observed in corallites. Thus, the generic attribution of this species is uncertain.
Distribution: Lower part of middle Upper Barremian (Rusalya).

Family INTERSMILIIDAE Melnikova et Roniewicz, 1976
Genus *Intersmilia* Eliášová, 1974
Type species: *Intersmilia malevola* Eliášová, 1974

Remarks: *Intersmilia* is a rare genus, known to occur since the Lower Jurassic (?Hettangian–Sinemurian; Melnikova and Roniewicz, 1976, 2002), but mostly from the Upper Jurassic/earliest Cretaceous (Eliášová, 1974; Roniewicz, 1976; Kołodziej, 2003; Roniewicz, 2008).

Intersmilia aff. *diaboli* Eliášová, 1974
Fig. 20

Material: One sample (ZPAL Bulg 3), eight thin sections.
Measurements (in mm): d = 6–8 (9), s = 12.
Remarks: With respect to corallite diameters, the specimen is similar to *Intersmilia diaboli* Eliášová [d = (6) 8–9 (10)]. However, the number of septa in *I. diaboli* is from 12 to 24 (S1–S3, sporadically S4). It is possible that septa S3 occur also in the specimen studied, but they are unrecognizable, owing to the state of preservation. The wall is dark in color, particularly in its outer part. The wall shows a rather complex, inner structure, but no double-layer structure as in *I. diaboli* was recognized. According to Eliášová (1974) *Intersmilia* displays intracalicular marginal budding. However the published pictures do not support this. It appears rather, as stated by Melnikova and Roniewicz (1976), that the budding is lateral. Parricidal budding was not observed by Eliášová (1974), neither in *I. diaboli*, nor in *I. malevola* Eliášová, 1974. It was recog- nized in one corallite of the sample, studied here, and in the Kimmeridgian *I. irregularis* Roniewicz, 1976 (see Melnikova and Roniewicz, 1976). In the specimen studied (Fig. 20C), as in *I. irregularis*, the septa of the parent individual continue into the daughter one (Melnikova and Roniewicz, 1976, fig. 4). Symmetry of the septal apparatus in *Intersmilia* was described by Eliášová (1974) as radial. However, pictures of *I. malveola* and particularly of *I. diaboli* (Eliášová, 1974, pl. 1, fig. 1, pl. 2, fig. 2, pl. 3, fig. 1, pl. 4, figs 1, 2) permit recognition of a longer, primary septum. Accordingly, the septal symmetry should be rather characterized as radio-bilateral.
Distribution: The sampling site can not be exactly located (Veliko Tarnovo or its close vicinity), therefore a general Barremian age is assumed for the studied specimen. *I. diaboli* is known from Tithonian–Lower Berriasian of the Štramberk Limestone.

Family HETEROCOENIIDAE Oppenheim, 1930

Remarks: The four species, described below, represent four phaceloid genera. In contrast to other pachythecaliines, the phaceloid growth form is rare in Heterocoeniidae. The systematic position of phaceloid genera *Cuneiphyllia* (one species; Eliášová, 1978) and *Pachythecophyllia* (one species; Kołodziej, 2003) from the Štramberk Limestone and Štramberk-type limestones respectively, originally attributed to the Heterocoeniidae, appears to be problematic, but certainly they represent pachythecaliines.

Genus *"Pseudopistophyllum"* Geyer, 1955
Type species: *Pseudopistophyllum berckhemeri* Geyer, 1955

Remarks: The new species, described below, is tentatively assigned to the genus *"Pseudopistophyllum"* Geyer, 1955. This species represents a new genus and was for the first time illustrated by Kołodziej *et al.* (2011b) and determined informally as Gen. nov. 2. sp. nov. 1. Recently Löser *et al.* (in press) proposed establishment of a new genus, based on a new species, recognized in the Upper Albian of Spain (see also Löser, 2009, fig. 101; Löser *et al.*, 2011). Apart from the Spanish and Bulgarian species, the new genus includes also the species, described from Slovenia by Turnšek (in Turnšek and Buser, 1976), as *Pseudopistophyllum quinqueseptatum*. This species was recognized in a limestone block of possible Late Jurassic age, occurring in Senonian breccias (Turnšek and Buser, 1976). The new genus differs from *Pseudopistophyllum* in having a different, septal pattern. In *Pseudopistophyllum* septa are developed on all sides of the wall, although the septa on one side are much longer. In the new genus, in specimens from Bulgaria, Slovenia and Spain, 3–5 septa are strongly developed on one side of corallites; other septa are absent, or if present, very rare and short (septal spines?). The genus is classified here in the Heterocoeniidae. In general, the septal pattern and poor developed septa of the new genus are similar to those, occurring in some heterocoeniids, such as *Latusastrea* and *Thecidiosmilia*. New buds were established in the wall of the parent corallite, but in contrast to amphiastraeids, further growth was outside of a calice of parent individuals.

"Pseudopistophyllum" triseptatum new species, Kołodziej
Fig. 21

2011b. Gen. nov. 2. sp. nov. 1. – Kołodziej *et al.*, fig. 1g, h.

Holotype: UJ 225P – Zar 996.
Paratype: UJ 225P – Zar 2-08.
Etymology: *triseptatum* – named after occurrence of three dominated septa.
Type locality: Zarapovo, Bulgaria.
Type level: Lower part of middle Upper Barremian, Emen Formation, Bulgaria.
Stratigraphic distribution: Lower part of middle Upper Barremian.
Diagnosis: *"Pseudopistophyllum"* with longer diameter ranging from (2) 2.5 to 3 (4) mm and a shorter one from (1.5) 2 to 2.5 (3) mm. Three, rarely four septa occur on one side of a corallite. Other septa are absent or very rare and short (septal spines?).
Material: Two samples (holotype UJ 225P – Zar 962, paratype UJ 225P – Zar 2-08), eight thin sections (two large).
Measurements (in mm): Long d = (2) 2.5–3 (4), small d = (1.5) 2–2.5 (3), s = 3–4; other septa rare or absent.
Description: Phaceloid corallum. Locally corallites are densely packed resulting in a pseudocerioid growth form. Septa rare, arranged in bilateral symmetry defined by 3–4 long septa on one side of the corallite wall. On the opposite side, septa (septal spines?) are absent or very rare and, if present, very short (septal spines?). The primary septum is usually strongest of all. In young corallites, only one septum can be recognized. A marginarium was recognized only in a few corallites. Endotheca unknown. New buds were established in a wall, but their growth, in contrast to Taschenknospung, was outside of the parent corallite.
Remarks: The new species differs from the one described by Löser *et al.* (in press; see also Löser, 2009, fig. 101) in having smaller corallite diameter, and in the number and character of the septa. In the species, described by Löser *et al.* (in press) there are 4–5 distinct septa, which have rhopaloid, T-shaped tips. *Pseudopistophyllum quinqueseptatum* has larger corallites (3–6 mm) and a unique, septal pattern, with 5 long septa, reaching almost the opposite side of the wall. As in some other pachythecaliines, in particular heterocoeniids, the number of septa is difficult to counted (e.g., Morycowa, 1971; Kołodziej, 1995, 2003; Löser, 2009; Löser *et al.*, 2009).
Distribution: Lower part of middle Upper Barremian (Zarapovo).

Genus *Heterosmilia* new genus, Kołodziej
Type species: *Heterosmilia spinosa* sp. nov., Kołodziej

Etymology: *Heterosmilia* – indicating its similarity to heterocoenid corals.
Stratigraphic distribution: Lower part of middle Upper Barremian.
Diagnosis: Phaceloid corallum. Bilateral, septal symmetry, with mostly distinct septa of subsequent orders. Primary septum displays strong, lateral outgrowths. Other septa lacking ornamentation. Lonsdaleoid septa present. Large dissepiments are clearly visible in transverse sections, but endotheca unknown. Budding extracalicular, lateral.
Remarks: The new genus shows similarities both with Heterocoeniidae as well as with Amphiastraeidae and even Intersmiliidae. Strong septal outgrowths are characteristic for many heterocoeniids (e.g., Kołodziej, 1995; Schöllhorn, 1998; Löser, 2008a, b, 2010), but are absent in amphiastraeids and intersmiliids. Transverse sections through the type species, i.e. *Heterosmilia spinosa* show some similarities to the solitary *Hexasmiliopsis* Löser, 2008 (see below remarks on *H. spinosa*).

Heterosmilia spinosa new species, Kołodziej
Fig. 22

2011b. Gen. nov. 1. sp. nov. 1. – Kołodziej *et al.*, fig. 1f.

Holotype: UJ 225P – Ru 20-09.
Paratype: UJ 225P – Ru 6-08.
Etymology: *spinosa* – named for spiny-like lateral outgrowths in the primary septum.
Type locality: Rusalya, Bulgaria.
Type level: Lower part of middle Barremian, Emen Formation, Bulgaria.
Stratigraphic distribution: Lower part of middle Upper Barremian.
Diagnosis: *Heterosmilia* with corallites of (7) 8–10 (11) in diameter. Septal pattern mostly regular: 6 S1 and 6 S2 in adult corallites. One or two sectors in some corallites are much wider than others. Septa S3, if developed, present only in two sectors on both sides of the primary septum.
Material: Four samples (UJ 225P – Ru 6-08, Ru 11-08, Ru 20-8, Ru 22-09), six thin sections (three large).
Measurements: Morphometric measurements are presented in Table 3.
Description: Phaceloid corallum. Septa arranged in bilateral symmetry defined by the presence of the primary septum, and in some corallites the presence of two wider sectors. In adult corallites, septal apparatus shows six septa S1 and six S2. Only two S3 are

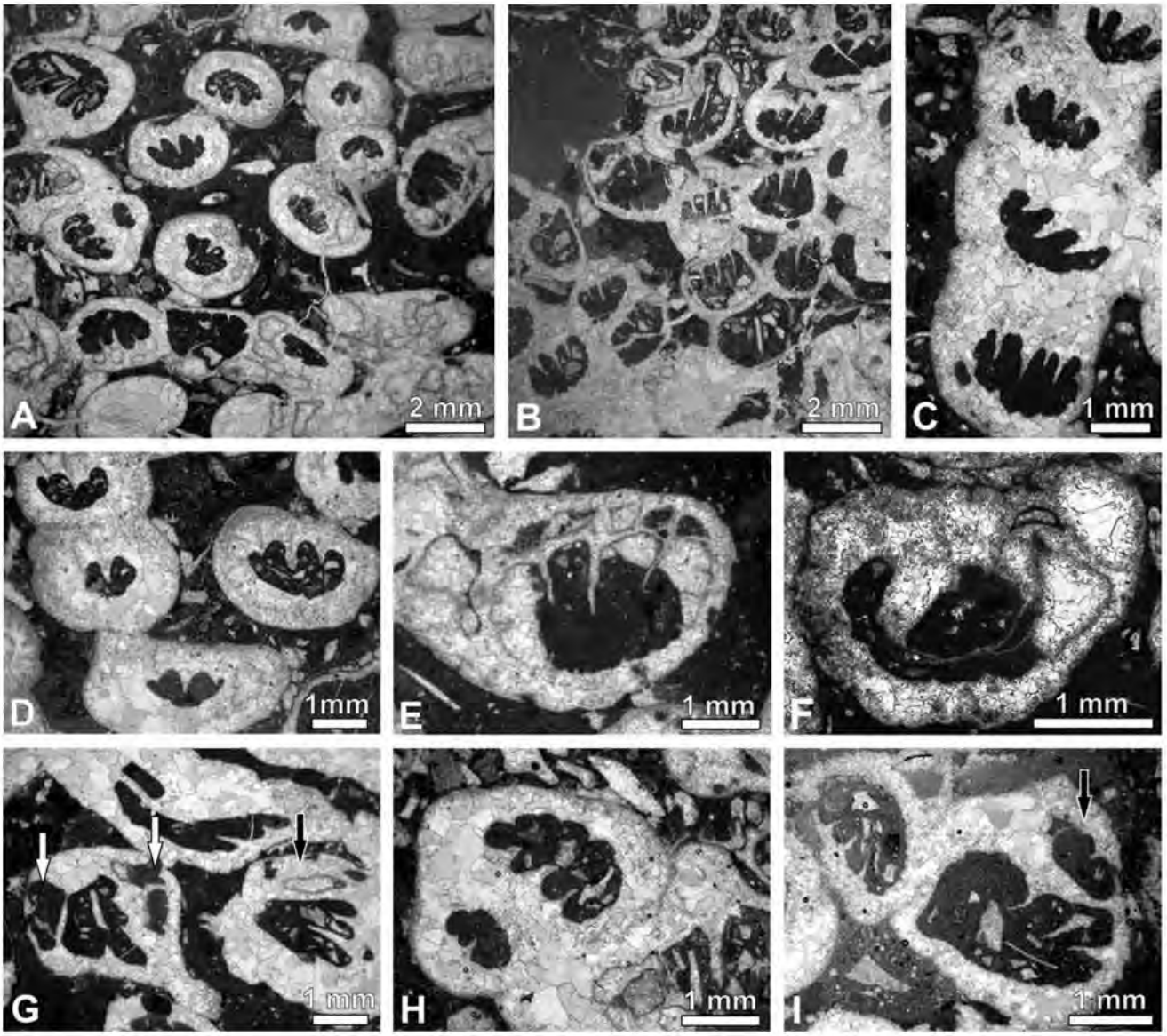

Fig. 21. "*Pseudopistophyllum*" *triseptatum* sp. nov. **A** – loose, phaceloid corallum. **B** – densely packed corallites. **C** –row of four corallites with 3–4 recognizable septa, arranged in same direction. **D** – corallites with thick wall and one prominent septum and two other poorly developed septa. **E, F** – corallites with poor marginarium. **G** – corallites with 'pockets' (arrows) in wall, which possibly correspond to early stage of new calice formation; further growth is external, as shown in **H** and **I** (arrow). UJ 225 P; A–E, H –Zar 996/6; F, I – Zar 2/08/1, G – Zar 996/5. A–E, G–H–holotype, F, I – paratype

developed in two wider sectors (if present) on both sides of the primary septum. Septa S2 in these two sectors are longer, giving impression that there are eight septa S1. Septa are thicker at the wall and thinner at the inner margin. A primary septum shows strong, septal outgrowths. Ornamentation on lateral faces of other septa is lacking. Large dissepiments present and may form regular zones (Fig. 22G). Endotheca unknown. On basis of relations of parent and daughter corallites, budding possibly is extracalicular, lateral.

Remarks: Dissepiments, observed in transverse section, are well developed. If the interseptal space is filled with sediment (not by calcite cement), it provides a better image of septal pattern and septal ornamentation. Transverse sections through *Heterosmilia spinosa* sp. nov. display similar corallite morphology and septal pattern, as in some transverse sections through the central part of the solitary heterocoeniid *Hexasmiliopsis saldanai* (Löser, 2008b, fig. 4a). Apart from the type specimens, two others (Ru 11-08, Ru 22-09) are attributed to this species. However, the poor state of preservation does not permit detailed measurements.

Distribution: Lower part of middle Upper Barremian (Rusalya).

Table 3

Dimensions (in mm) of *Heterosmilia spinosa* sp. nov.

Sample number	d	s
Holotype UJ 225P - Ru 20-09	(8) 9–10 (11)	12 +S3
Paratype UJ 225P - Ru 6-08	(7) 8–10	12? +S3

Genus *Hexasmilia* de Fromentel, 1870

Type species: *Hexasmilia ferryi* de Fromentel, 1870

Remarks: This poorly known genus (Upper Barremian–Santonian) was recently reviewed by Löser (2008a). *Hexasmilia* differs from *Heterocoenia* Milne Edwards and Haime, 1848 in its phaceloid growth form and the presence of strong septal outgrowths.

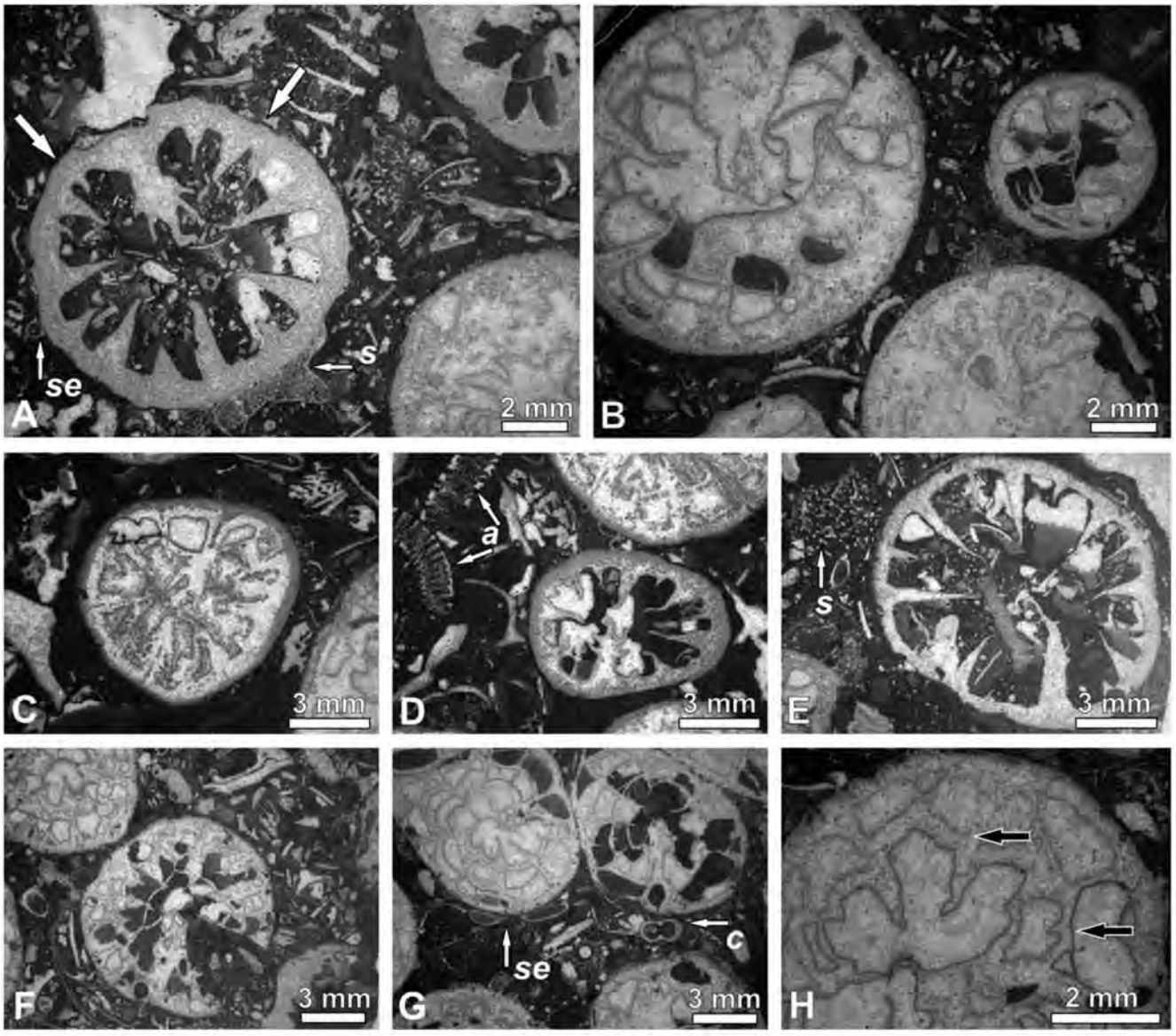

Fig. 22. *Heterosmilia spinosa* gen. et sp. nov.; A–E – holotype, UJ 225 P – Ru 20; F–H – paratype, UJ 225 P – Ru 6-08. **A** – corallite with 6 septa S1, 6 S2; note that only in two sectors (arrows) septa S3 are developed. See also different size of sectors on E. **B–H** – transverse sections, showing corallites with well preserved (B, F, G, H) and not preserved (C–E) dissepiments. Arrows on H show lonsdaleoid septa. Microfossils: *s* sponge, *se* serpulids, *a* dasyclad alga *Zittelina hispanica* Masse, Arias et Vilas, *c* remain of crustacean *Carpathocancer? plassenensis* (Schlagintweit et Gawlick). A–B – Ru 20/1, C–D – Ru 20/2, E – Ru 20/3, F–H – Ru 6-08/1

Three species were included by Löser (2008a): *H. ferryi* de Fromentel, *H. pachythecalia* (Kuzmicheva, 1980), and new species *H. elmari*.

?*Hexasmilia* sp.
Fig. 23

Material: One sample (UJ 225P – Ru 7862), three thin sections (one large).
Dimensions (in mm): d = (5) 6–7, s = 12 + S3.
Remarks: The specimen from Bulgaria is similar to *Hexasmilia elmari* Löser, 2008, which shows some variability, expressed in differentially developed, septal apparatus. The specimen studied displays transverse sections, similar to *H. elmari* (compare Löser, 2008a, fig. 4, fig. 5.6, 5.8; and Fig. 23A, B in this paper) with six S1, including a primary septum. In other sections of *H. elmari* (Schöllhorn, 1998, pl. 21, fig. 8; Löser, 2008a, fig. 5.1, 5.4, 5.5), there is a prominent, primary septum with strong septal outgrowths, while other septa are poor and less regularly developed. It is possible that more thin sections through the Bulgarian specimen will reveal greater, morphological variability. The septal division, observed by Löser (2008a) in *H. elmari*, was not observed in the specimen studied.
Distribution: Lower part of middle Upper Barremian (Rusalya).

Genus *Hexapetalum* Eliášová, 1975
Type species: *Hexapetalum impium* Eliášová, 1975

Remarks: The poorly known genus *Hexapetalum* was originally placed by Eliášová (1975) among the Amphiastraeidae, later in the separate family Hexapetallidae (Eliášová, 1976b; Kuzmicheva, 1980). Kołodziej (2003) transferred this genus to the Heterocoeniidae.

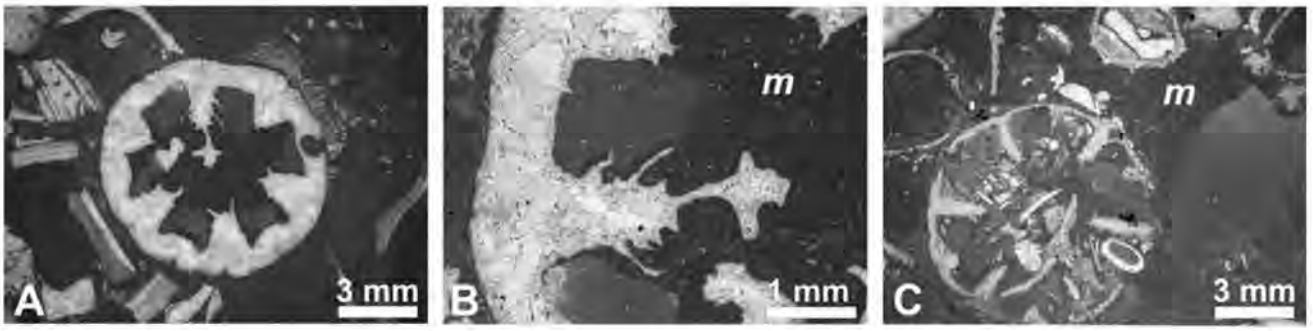

Fig. 23. *?Hexasmilia* sp. **A** – transverse section of corallite, with thick septa S1 and septal outgrowths, particularly strongly developed on primary septum (**B**). **C** – corallite with different, septal pattern (lack internal invaginations of the wall); *m* on B, C indicate microbialite crusts. UJ 225 P; A, B –Ru 7862/1, C – Ru 7862/2

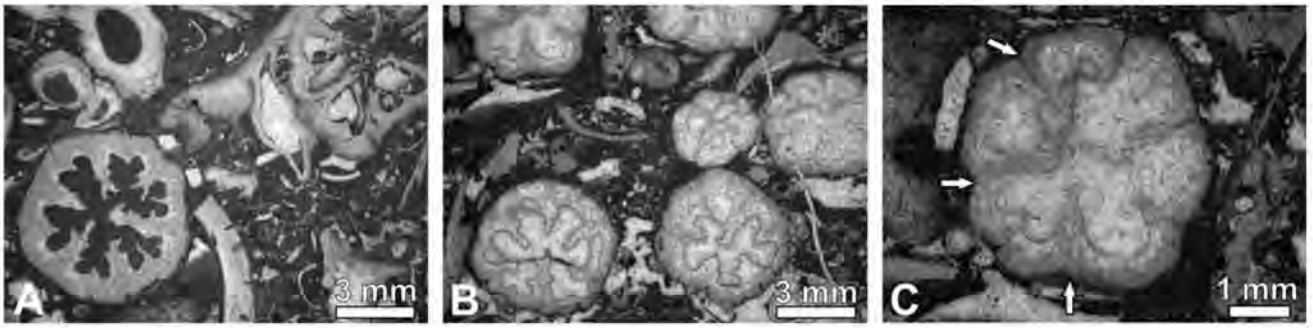

Fig. 24. *?Hexapetalum* sp.; **A** – transverse section of corallite with thick septa S1 and distinct, granular, septal ornamentation; UJ 225 P – Ru 2-08/1. **B, C** – corallites, showing external concavities of wall (arrows on C); UJ 225 P – Ru 40-08/2

?Hexapetalum sp.
Fig. 24

Material: Three samples, six thin sections.
Measurements: Morphometric measurements are presented in Table 4.

Table 4

Dimensions (in mm) of *?Hexapetalum* sp.

Sample number	d	s
UJ 225P - Ru 40-08	4 (5)	6S1 + S2 +S3
UJ 225P - Ru 2	(4) 5 (6)	6 S1 + S2 +S3
ZPAL Bulg 2	(3) 4–5 (6)	6 S1 + S2

Remarks: Six septa S1 are well developed. Septa S2 are poorly and irregularly developed, septa S3 very rare or absent. One septum S1 is more or less longer. In a poorly preserved specimen Bulg 2, only six septa S1 are recognizable. Septa S1, if well preserved, show septal outgrowths or spiny ornamentation. Budding lateral, extracalicular. Wall morphology in some corallites display external concavities and internal invaginations, corresponding to septa (Fig. 23B, C). In this respect, the specimens described are similar to *Hexapetalum impium* Eliášová, *H. pium* Eliášová (Eliášová, 1975, pl. 9, fig. 2a; Eliášová, 1976b, pl. 2, figs 2, 3; Kołodziej, 2003, fig. 21), *H. pachythecallium* Kuzmicheva and *Heteroceonia* spp. (Beauvais, 1982; Baron-Szabo, 1998; fig. 2; Löser, 2009, fig. 174). In particular, in *Hexapetalum pium*, the septa and wall show clear, structural continuity. The specimen, described here, has strong, septal, granular ornamentation (in well preserved corallites), in which it differs from other corals, described as *Hexapetalum*.
Distribution: lower part of middle Upper Barremian (Rusalya); Barremian (Veliko Tarnovo or its close vicinity).

CONCLUSIONS

1. The Upper Barremian limestones of the Emen Formation of the Lovech Urgonian Group in the Veliko Tarnovo area (Fore-Balkan, northern central Bulgaria) contain bioconstructions (possibly mostly biostromes) with a distinctive coral community, dominated by diversified corals of the extinct suborder Pachythecaliina. Its higher systematic position is debatable, but following some other coral specialists, these corals are classified here not in the Scleractinia, but in the order Hexanthiniaria. The corals described are mostly of the phaceloid growth form, with *Pleurophyllia bulgarica* sp. nov. particularly frequent. Other corals, except for the phaceloid *Calamophylliopsis*, are rare.

2. Small, monopleurid, cylindrical rudists *Mathesia darderi*, frequently densely clustered, and non-laminated microbialites provided additional, structural support for bioconstruction growth. Other macrofauna are only moderately common and diversified. *Lithocodium aggregatum* (possibly chlorophycean alga) and microbial, 'bacinellid' structures are rare, although they are common in many other coral-bearing limestones of the Lovech Urgonian Group.

3. The association of phaceloid pachythecaliine corals and *M. darderi*, accompanied by microbialites, is unique,

worldwide. The resulting bioconstructions are known only from the Emen Formation and show limited, regional extent, from Veliko Tarnovo to about 20 km NW. Biostratigraphic data indicate that this biofacies was developed, mainly during the early middle Late Barremian (Gerhardtia sartousiana Zone).

4. The section at the Rusalya Quarry, about 42 m thick provides, the sedimentary and environmental context of the reefal biostromes. Bioclastic packstones of unit 1 contain small boundstone patches, with corals (but not pachythecaliines or other branching corals), calcified sponges (mainly chaetetids) and encrustations of *L. aggregatum*. Units 2 and 3 consist of bioclastic limestones (rare corals) interlayered with rudist limestones. Pachythecaliine-*Mathesia*-microbialite biostromes (unit 4) developed in a narrow 2.5-m-thick interval, are covered by biostromes, built mostly of large, monopleurid rudists (unit 5). The sedimentary succession shows, with some fluctuactions, a general shallowing trend, from the outer to inner carbonate platform. Pachythecaliine-rich biostromes were developed on the distal part of the rudist-dominated area of the carbonate platform, in a low-energy setting, with low rates of net, background sedimentation and possibly a higher nutrient level. This environment favoured growth of phaceloid pachyhecaliines, a nearly monospecific rudist community (*M. darderi*), and microbialite development, but limited growth of phototrophic/oligotrophic microencrusters.

5. It is hypothesized that some of microbialites (*sensu lato*) resulted from decaying sponges. Dolomite, recognized in the microbialites (Vishovgrad site), is interpreted as resulting from precipitation, linked to microbial activity or organomineralization *s.s.*

6. Taxonomic diversity and abundance of phaceloid pachythecaliines show a spatially and temporally restricted pattern. They are only more common in the Tithonian–Lower Berriasian Štramberk Limestone (Czech Republic) and its equivalent in the Polish Carpathians. However, the lithology and associated biota imply that pachythecaliines from the Emen Formation developed in a different, environmental setting. Other coral-bearing deposits of the mixed, siliciclastic-carbonate Urgonian complex in Bulgaria contain diversified coral communities, but pachythecaliines are very poorly diversified and phaceloid pachythecaliines are absent.

7. Fourteen species (including six new and eight in open nomenclature), representing twelve genera (four new, three of them are distinguished formally) and five families (Amphiastraeidae, Carolastraeidae, Intersmiliidae, Donacosmiliidae, Heterocoeniidae), are described. Four heterocoeniid species (two new) from four genera (one new) are phaceloid, thus displaying a growth form, generally rare in this family. This suggests similar, environmental demands for phaceloid heterocoeniids and other phaceloid pachythecaliines and may support phylogenetic relationships between them.

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